

1 **The use of pigs vocalisation structure to assess the quality of** 2 **human-pig relationship**

3 **Authors**

4 Avelyne S Villain* [1, 2], Carole Guérin [1], Céline Tallet* [1]

5 **Affiliations**

6 [1] PEGASE, INRAE, Institut Agro, 35590 Saint Gilles, France

7 [2] Behavioural Ecology Group, Section for Ecology & Evolution, Department of Biology,
8 University of Copenhagen, 2100, Copenhagen Ø, Denmark

9 * **Corresponding authors** : avelyne.s.villain@protonmail.com, celine.tallet@inrae.fr

10 **Key words**

11 Positive handling, Acoustic communication, Emotions, Mood, Behaviour, Welfare, Interspecific
12 interactions.

13 **Abstract**

14 Studying human-animal interactions in domestic species and how they affect the establishment of a
15 positive Human-Animal Relationship (HAR) may help us improve animal welfare and better
16 understand the evolution of interspecific interactions associated with the domestication process.
17 Understanding and describing the quality of an HAR requires information on several aspects of the
18 animal biology and emotional states (social, spatial and postural behaviours, physiological and
19 cognitive states). Growing evidence shows that acoustic features of animal vocalisations may be
20 indicators of emotional states. Here, we tested the hypothesis that vocal structure may indicate the

21 quality of HAR. At weaning, 30 piglets were positively handled by an experimenter who talked to
22 and physically interacted with them three times a day, while 30 other piglets only received the
23 contact necessary for proper husbandry. After two weeks, we recorded the behaviours and
24 vocalisations produced in the presence of the static experimenter for 5 min. We repeated this test
25 two weeks later, after a conditioning period during which human presence with additional positive
26 contacts was used as a reward for all piglets. We hypothesized this conditioning period would lead to
27 a positive human-piglet relationship for all piglets. As expected, piglets that were positively handled
28 at weaning expressed a higher attraction toward the experimenter, and, after the conditioning, piglets
29 that were not positively handled at weaning expressed a similar level of attraction than the positively
30 handled ones. Piglets positively handled at weaning produced shorter grunts than the other ones,
31 regardless of the context of recording, which may indicate a more positive affect. During reunions
32 with the static experimenter, a more positive HAR was associated with a decrease in vocal reactivity
33 to human proximity. However, during reunions with the experimenter providing additional positive
34 contacts and over the conditioning, proximity to the human systematically triggered shorter and
35 higher pitched grunts, indicator of positive a emotional state. Results first show that changes in vocal
36 structure are consistent with indicators of positive states in the presence of a human. Second, these
37 changes are stronger when the human positively interact with the piglets, supposedly emphasizing a
38 higher positive arousal state during these interactions. We show that vocalisation structure may be a
39 promising indicator of the quality of human-pig relationship.

40 **Introduction**

41 The process of domestication was conducted to shape physiology and morphology of domestic
42 animal species, but also their behaviour. It notably has shaped interspecific interactions between
43 human and non-human animals, by improving animals' capacity to use human signals to adapt their
44 behaviour both decreasing fearfulness toward humans and increasing attention toward humans
45 (Mignon-Grasteau et al., 2005). In farms, the relationship that domestic animals form with humans is
46 important for animal welfare. Therefore, studying human-animal interactions and their consequences
47 to understand the mechanisms of emergence and maintenance of a positive human-animal
48 relationship (HAR) directly applies to welfare (Rault et al., 2020). Animal welfare consists of three
49 major aspects: the ability of an animal to control its mental and physiological stability (Broom,
50 2011), the decrease of experiencing negatively perceived contexts and the increase in experiencing
51 positively perceived contexts and species-specific behaviors (Peterson et al., 1995; Weerd & Day,
52 2009). A positive HAR is thought to be established through repeated positive interactions between
53 the human and the non-human animal. Some of the mechanisms involved in this process are:

54 accumulation of positive experiences through positive associative learning, modifications of
55 cognitive biases, shaping expectations from the non-human animal toward the human. A positive
56 HAR can be appreciated through behavioural and physiological measures, for example by assessing
57 the expression of positive emotions [reviewed in (Rault et al. 2020)]. Several behavioural measures
58 may help to define a positive HAR such as: short latency to approach and spatial proximity (Boivin
59 et al., 2000; Schmied et al., 2008), body postures (Villain, Lanthony, et al., 2020) or play behaviour
60 (Jerolmack, 2009). Contacts from a human such as stroking, may induce changes in body postures
61 and exposition of body areas by the animal to the human, supposedly vulnerable [central neck area in
62 cattle (Schmied et al. 2008), abdominal area in pigs (Rault et al., 2019)]. Such grooming solicitation
63 may be markers of engagement, trust and motivation to interact with the human. In most cases, these
64 behaviours are similar to those shown during intraspecific socio positive interactions, although there
65 are some species specific behaviours [e.g., dog vs. wolf (Gácsi et al., 2005)]. Vocal behaviour may
66 also help defining the quality of an HAR. First, some vocalisations type have been associated with
67 positive interactions with humans, for example the cat – human communication : purring is thought
68 to be derived from mother pup communication during nursing and is observed associated with care
69 solicitation from humans; meowing, which is not observed during intra specific interactions is
70 thought to emerge from associative learning during cat – human interactions (Brown & Bradshaw,
71 2014). This shows that HAR may elicit specific vocalisations from the non human animal toward the
72 human. Second, vocalisation structure is known to carry markers of the emotional states in several
73 bird and mammal species (Briefer, 2012, 2020) and markers of emotional valence (positive versus
74 negative) has been studied in domestic farm animals [reviewed in Laurijs et al. (2021)]. Since
75 positive or negative HAR is likely to affect the emotional state of animals, it is likely that it may be
76 reflected in the structure of the produced vocalisations.

77 In pigs, diversified evidence attest the possibility of a positive HAR. Animals may be handled by
78 humans providing regular additional positive contacts, leading to the expression of a positive
79 perception of humans, with evidence from behavioural and physiological studies. Cognitive bias tests
80 showed a positive judgment bias in piglets that had received gentle contacts with humans (Brajon et
81 al., 2015b). Pigs may recognise a human providing positive contacts compared to an unfamiliar one
82 and adapt their behaviour accordingly (Brajon et al., 2015c). Pigs may be sensitive to human voice
83 and respond accordingly (Bensoussan et al., 2019, 2020). Pigs vocalisations are diverse and linked to
84 their emotional states, attested by the use of positive or negative call types (Briefer et al., 2019, 2022;
85 Tallet et al., 2013). In addition, even within a call type, spectro-temporal changes are closely related
86 to the valence or the arousal a situation may trigger for the animal. For example, the grunt, a contact
87 call, is used in various contexts and is now known to be a flexible call. Positive situations have been
88 associated with shorter grunts compared to negative ones (Briefer et al., 2019, 2022; Friel et al.,

89 2019), as well as higher formants (which are frequency peaks containing more energy than others)
90 and a lower fundamental frequency during positive situations (Briefer et al., 2019, 2022). Grunt
91 structure may also change according to the arousal of a negative situation: the higher the arousal in
92 the negative state the higher the frequency range and bandwidth (Linhart et al., 2015) and the longer
93 (Puppe et al., 2005) the grunts. Variation in grunt spectro-temporal structure in positive situations of
94 different arousal is still unknown.

95 In order to determine to what extent vocalisations structure could be used as non invasive indicator
96 of the quality of human-pig relationship, we tested whether varying the degree of familiarity and the
97 quality of the human-pig interactions could modulate the spectro-temporal structure of vocalisation,
98 through the vocal expression of emotional state. Because it was suggested to study vocal markers of
99 emotions within the same call type (Briefer, 2020) and because grunts are the most commonly
100 produced call in various contexts, we studied the spectro-temporal structure of grunts. We predicted
101 that if grunts reflect the quality of the human-pig relationship, then 1. A period of positive handling
102 given by a human should modulate piglets vocal expression in presence of the human, leading to
103 grunts exhibiting markers of positive states (higher pitched and shorter grunts), 2. Spatial proximity
104 toward the human should influence the spectro-temporal structure of grunts (higher pitched and
105 shorter grunts).

106 **Methods**

107 Ethical note

108 The study was approved by the ethic committee CREEA and received the authorization no.
109 APAFIS#17071-2018101016045373_V3 from the French Ministry of Higher Education, Research
110 and Innovation. UE3P, where the experiment was carried out, is an experimental unit authorized by
111 the French Ministry of Agriculture to breed animals for experimentation under the number D35-275-
112 32. This authorization includes a derogation to follow the directive 2008/120/EC relative to the
113 protection of piglets and its regulations.

114 Subjects and housing conditions

115 Sixty weaned female pigs (in two replicates from January to April 2019), *Sus scrofa domesticus*,
116 bred from crosses between Large White and Landrace females and Piétrain males were used for this
117 study from 28 to 62 days after birth. Animal housing and experiments took place at the experimental
118 unit UE3P (UE 1421, INRAE France).

119 One piglet had to be excluded from our sample size to receive care/medication due to health issues
120 independent from the experiment. From weaning at 28 days of age, piglets from the same litter and
121 having similar weight (<1 kg difference) were housed by three in a 1.2 x 1.3m pen on plastic
122 duckboard. Wooden panels were used to visually isolate pens. One metal chain per pen was used for
123 enrichment. Food and water were available *ad libitum*. Artificial lights were turned on from 8:00 to
124 17:00 and temperature was maintained between 26 and 27 °C. The experiment was carried out in two
125 replicates and two identical rearing rooms were used (5 pens per room per replicate).

126 Treatment: positive handling at weaning

127 From day 28 (day of weaning) to day 39 of life, piglets were separated into two groups that
128 experienced a different post-weaning period as follows:

129 - **Non positively handled piglets (H piglets):** Control piglets from 10 rearing pens, housed in the
130 same room, received the minimal amount of daily contact with a stockperson (a 1.70m tall male who
131 did the feeding, cleaning and health checkups). The stockperson wore a dark green shirt and pants
132 and brown shoes.

133 - **Positively handled piglets piglets (H+ piglets):** Experimental piglets from the 10 other rearing
134 pens, housed in another room, received the same daily care given by the same stockperson as for H
135 piglets. They additionally received repeated sessions of additional human contacts. Each pen of three
136 piglets received 29 sessions of 10 min , from day 28 (weaning) until day 39, occurring five days a
137 week. Three sessions per day were performed (except on the day of weaning during which only two
138 were done with a two-hour break in between). Each session took place in the rearing pen and the
139 order of the interventions in the pens was balanced across days. The handling procedure, using gentle
140 tactile contacts is described in supplementary material of Villain et al. (2020) and was similar to
141 Tallet et al. (2014). Briefly, the behaviour of the human toward the piglet was adapted to the reaction
142 of each animal and included four steps: (1), the handler hold out the hand towards the animal; (2) if
143 the piglet did not move away, the handler tried to touch it; (3) if the piglet accepted being touched,
144 the handler softly stroked it along the body with the palm of her hand; and (4) once it accepted being
145 stroked, the handler scratched it along the body with her fingers. Scratching consisted in rubbing the
146 skin of the piglets with the finger tips and applying more pressure than stroking. No specific body
147 part of the piglets was more considered than another. Two experimenters ('AV' and 'AH') performed
148 these sessions (both women, both between 1.70-1.73 m tall, with a balanced number of pens
149 attributed to each of them). The experimenters wore the same blue overalls and green boots each

150 time they interacted with the piglets. The experimenters tried to imitate each others behaviours
151 (remote video monitoring) to decrease variability.

152 This intense period of additional positive contacts for half of the piglets after weaning constituted the
153 treatment of positive handling at weaning: positively handled piglets are referred to as H+ piglets and
154 non positively handled piglets are referred to as H piglets to describe the early experimental
155 treatment they experienced regarding a human, prior to the conditioning.

156 Conditioning: sessions of additional positive contacts with 157 (un)familiar human

158 The conditioning took place between day 42 and 62 of age and lasted twelve days, with two trials
159 per day and at least three hours between trials on the same day. Piglets were habituated to the test
160 room for 10 min, by pen, two days before the start of the conditioning. All piglets (H and H+) were
161 subjected to the same conditioning. The experimental design of the conditioning is already published
162 in an article dedicated to the study of anticipatory behaviour (Villain, Hazard, et al., 2020).

163 Briefly, all piglets were individually trained to learn to associate two different stimuli with the
164 arrival of two different (pseudo)-social partners: either two pen mates (partner = Conspecifics) or a
165 familiar human (partner = Human). When entering the room, the piglets and the partner(s) would
166 remain in the room for 2 min. Specifically, when the human was the partner, the human entered, sat
167 on a bucket and positively interacted with the piglet for 2 min, in the same manner as additional
168 contacts was provided to the H+ piglets during the previous period (see above section) (figure 1).
169 Therefore, at the beginning of the conditioning, H+ piglets were already familiar with the human and
170 procedure, whereas H piglets were unfamiliar with the human. During the conditioning, the same
171 sessions occurred in both treatment groups (H and H+). After the conditioning, all piglets were
172 familiar with the human, but treatment groups had a different time of exposure to them. Sessions of
173 reunions with social partners were not studied here because they were part of an analysis on vocal
174 expression of positive anticipation reported earlier (Villain, Hazard, et al., 2020).

175 For every second trial, the 2 min reunions with the human were analysed by the same person: trials
176 number 2, 4, 6, 8, 10 and 11 (see behavioural analyses section).

177 Standard Isolation/Reunion Tests with a static and silent human

178 At 40 or 41 (before conditioning) and then 63 or 64 (after conditioning) days of age, piglets were
179 subjected to a standard Isolation/Reunion test in order to assess their perception of the human. The
180 test consisted of two phases. The piglet was brought individually in a trolley to the experimental

181 room. It was left alone for 5 min, which defined the ‘Isolation’ phase. Then, the human entered the
 182 room, remained stand up for 30 seconds and they sat on a bucket, remaining silent and not moving
 183 for 4.5 min (figure 1).

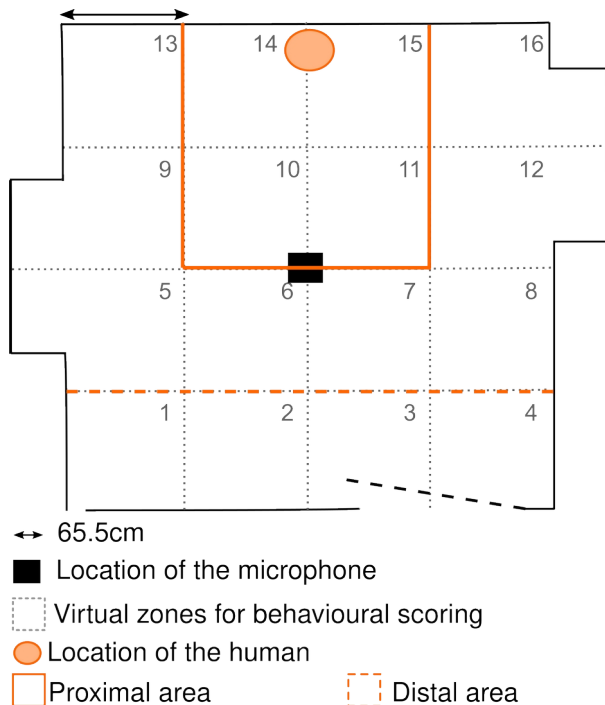


Figure 1: Design of the room used during the Isolation/Reunion tests and the additional positive contacts sessions of the conditioning. The room was split into 16 virtual zones. A proximal area (zones 10, 11, 14, 15) and a distal area (zones 1, 2, 3, 4) were defined, using the location of the human as reference. Behavioural monitoring and analyses

184 Sessions and tests were recorded using a camera (Bosh, Box 960H-CDD) and behaviours were
 185 scored *a posteriori* on videos using *The Observer XT 14.0* (Noldus, The Netherlands) software. The
 186 room was split into 16 virtual equally-dimensioned zones to assess the mobility and exploratory
 187 behaviour of the piglet. A proximal area, around the human was defined by merging four zones, a
 188 distal area was defined merging the four most distant zones from the human (figure 1).

189 The behaviours scored during the reunion of the Isolation/Reunion test and the sessions of
 190 additional positive contacts of the conditioning are available in table 1. Every time the shoulders of
 191 the piglet crossed a zone, a zone change was scored. Looks and watching behaviours were scored as
 192 point events, all other behaviours were scored as state events. Behavioural scores were then
 193 calculated to quantify global responses (see Table 1).

Table 1: Ethogram.

Behaviour	Description
No. zones crossed ^{1,2}	The number of times the piglet crossed a virtual zone
No. approaches H ¹	Number of times the piglets entered the proximal area
Time watching H ^{1,2}	The amount of time the piglet spent watching the human
Latency to contact H ^{1,2}	The latency to the first contact of the human by the piglet

No. looks toward H ^{1,2}	The number of times the piglet turned its head toward the human
No. looks at walls and doors ¹	The number of times the piglet looked at walls and doors
Time watching walls and doors ¹	The amount of times the piglet watched walls and doors
Time in proximal area ^{1,2}	The amount of time the piglet spent in the proximal area
Time in distal area ^{1,2}	The amount of time the piglet spent in the distal area
Time in contact H ^{1,2}	The amount of time the piglet investigated the human
Time investigating floor ^{1,2}	The amount of time the piglet investigated the floor
No. contacts H ²	Number of times the piglet was in contact with the human (initiated by the piglet or the human)

¹: Scored during reunions of Isolation/Reunion tests. ²: Scored during reunions of conditioning sessions

194

195 Acoustic monitoring and analyses

196 Vocalisations were recorded with an AKG C314 microphone placed in the center of the room and
 197 one meter above the ground, connected to a Marantz MD661MK2 recorder. Vocalisations produced
 198 during each phase of the trial were manually annotated according to vocal type (grunt, squeal, bark,
 199 scream and mixed calls (Kiley, 1972)), after visual inspection of spectrograms using the ‘Annotate’
 200 function of the Praat software (Boersma & Paul, 2001), version 6.0 from <http://www.praat.org/>.
 201 Checking the occurrence of each call type in the several contexts of the study, we confirmed that
 202 ‘grunt’ was the call type used in all contexts and by most of the piglets in each context. So only the
 203 spectro-temporal structure of grunts was further analysed. For information, a table of the number of
 204 each call types recorded in each context as well as the number of individuals involved in the count is
 205 presented in the electronic supplementary material. We could not conduct a robust statistical analysis
 206 on call type utterance, due to the rarity (per subject and tests) of other vocalisations than grunt. (table
 207 S5).

208 A spectro-temporal analysis was performed with custom-written codes using the Seewave R
 209 package (Sueur et al., 2008) implemented in R (R Core Team, 2022). We first studied the spectral
 210 properties of the remaining background noise of the experimental room (electric noises and
 211 remaining low frequency noises from the rest of the building), using 20 examples of 0.5 second
 212 fragments and compared it with the general frequency range of the grunts. To avoid measuring
 213 masking effect of the background noise, grunts were filtered using a 0.2-8 kHz bandpass filtering
 214 (‘fir’ function). As a consequence, all results presented in this study are on a 0.2-8 kHz frequency
 215 range, and no conclusions on frequency components of grunts below this 200 Hz threshold are drawn
 216 here. Several acoustic parameters were then extracted from each grunt. To measure grunt duration, a
 217 5% to maximal amplitude threshold was used (‘timer’ function). After normalisation, the following
 218 spectral parameters were calculated using the ‘specprop’ function (FFT with Hamming window,
 219 window length = 512, overlap = 50%): mean (Q50), first (Q25) and third (Q75) quartiles,

220 interquartile range (IQR), centroid and standard deviation (all in Hz). The grunt dominant frequency
 221 (in kHz) was also calculated ('dfreq', 50% overlapping FFTs, window length = 512), which is the
 222 mean over the grunt duration of the frequencies of highest energy of each window. Frequency peaks
 223 were detected and the minimal and maximal peaks were kept as descriptors ('fpeaks' function,
 224 window length = 512, peak detection threshold = 10% of the normalized amplitude). Measures of
 225 noisiness and entropy of the grunts were assessed using: Shannon entropy (sh), Spectral Flatness
 226 (Wiener entropy, sfm) and Entropy (H) [combining both Shannon and Temporal envelop entropy,
 227 length = 512, Hilbert envelop). Two vocal scores were used: the logarithm of grunt duration and a
 228 built-in spectral vocal score with all spectral parameters (see below). A table describing mean and
 229 range of variation of each acoustic parameter in the relevant contexts of the study is available in the
 230 supplementary material (table S4).

231 Statistical analyses

232 ***Behavioural and vocal response scores***

233 All measures extracted from videos or sound analysis are named parameters throughout the text.
 234 The symmetrical distribution of parameters (behavioural on the one hand and acoustic on the other
 235 hand) was visually inspected, and linear transformations were computed when necessary to reach
 236 symmetrical distribution (see tables 2, 3, 4). When this criteria was reached, Principal Component
 237 Analyses (PCA, one for the behavioural analysis and one for the spectral acoustic analysis) were
 238 performed using several parameters to build scores ['dudi.pca' function from 'ade4' R package
 239 (Dray & Dufour, 2007) and 'inertia.dudi' function to extract the loadings]. These scores were then
 240 used as statistical variables. Indeed, PCAs are generally used to reduce the number of variables
 241 included in statistical models. It also generates quantifiable global descriptors of behaviours or
 242 acoustic structure, since correlated parameters usually load on the same PC (McGregor, 1992). All
 243 PCs having an eigenvalue above one were kept and constituted response scores of behavioural
 244 ('ReuPCs' and 'CondPCs' in table 2 and 3 respectively) and vocal ('VocPCs', table 4) parameters.
 245 Only the duration of grunts was kept separated from the spectral parameters to keep it as a temporal
 246 parameter.

Table 2: Percentage of explained variance and relative loadings of parameters on PCs, following the Principal Component Analysis computed on the behaviours scored during the reunion of the Isolation/Reunion test. The first three PCs, having an eigenvalue above 1, constituted three behavioural scores: ReuPC1, ReuPC2, ReuPC3. Parameters that explain the most each PC are bolded ($|loading| > 0.4$).

ReuPC1

ReuPC2

ReuPC3

Cumulative variance explained %	38.3	60.8	74
No. of zones crossed (sqrt)	24.177	-55.843	-0.435
No. approaches H (ln)	47.748	-30.163	0.578
Time watching H (ln)	-52.914	-7.422	25.585
Latency to contact H (ln)	-64.232	-0.464	1.688
No. looks toward H (sqrt)	-7.787	-43.721	31.633
Time watching room	-32.048	-13.581	-6.238
No. looks at walls and doors (sqrt)	3.524	-72.408	-2.027
Time in proximal area (sqrt)	69.96	-0.156	9.584
Time in distal area (sqrt)	-46.416	-12.437	-1.215
Time in contact H (sqrt)	61.041	3.586	24.183
Time spent investigating floor	11.868	-7.503	-42.265

247

Table 3: Percentage of explained variance and relative loadings of parameters on PCs, following the Principal Component Analysis computed on the behaviours scored during the sessions of additional positive contacts of the conditioning. The first three PCs, having an eigenvalue above 1 constituted three behavioural scores: CondPC1, CondPC2, CondPC3. Parameters that explain the most each PC are bolded ($|\text{loading}| > 0.4$).

	CondPC1	CondPC2	CondPC3
Cumulative variance explained %	41	68.5	80.7
Time in proximal area (ln)	80.23	2.542	-0.112
Time in distal area (ln)	-33.826	8.547	30.789
Number of contacts H (ln)	78.55	6.476	2.288
Time in contact H (ln)	86.625	0.715	-0.369
No. looks toward H (ln)	-2	79.898	-0.745
Time watching H (ln)	-6.757	65.67	-10.325
No. of zones crossed (sqrt)	0.129	33.599	48.457
Time spent investigating floor	0.006	-49.286	14.205
Latency to contact H	-81.01	-0.248	-2.83

248

Table 4: Percentage of explained variance and relative loadings of parameters on PCs following a Principal Component Analysis on spectral parameters of the grunts recorded in the entire dataset (including both types of tests, $N=17\ 546$ grunts). The transformations used to reach symmetrical distribution before the PCA are indicated in parentheses. The first three PCs, having an eigenvalue above 1 constituted three vocal response scores: VocPC1, VocPC2, VocPC3. Parameters that explain the most each PC are bolded ($|\text{loading}| > 0.4$).

	VocPC1	VocPC2	VocPC3
Cumulative variance explained %	59.769	76.807	87.712

Mean Dominant Frequency ¹	-13.558	53.557	2.220
Min frequency peak ¹ (ln)	-0.349	58.758	24.236
Max frequency peak ¹	-43.023	8.760	-9.537
Mode ² (ln)	-0.522	66.248	19.268
Mean ² (ln)	-95.092	-2.295	2.028
Q50 ² (ln)	-85.278	0.280	-0.093
Q25 ² (ln)	-52.360	19.327	0.985
Q75 ² (sqrt)	-88.925	-4.645	2.309
Centroid ² (ln)	-95.092	-2.295	2.028
Sd ²	-64.484	-11.303	7.680
IQR ²	-87.981	-5.851	2.640
Sfm ³ (sqrt)	-94.344	-3.189	0.962
Sh ³ (sqrt)	-96.087	-0.785	-0.175
H ³	-88.205	-1.059	-1.063
Skewness ⁴	28.032	-18.010	48.652
Kurtosis ⁴	22.973	-16.241	50.615

¹: parameters related to the pitch of the vocalisation; ²: parameters related to the frequency distribution descriptors; ³: parameters related to the noise component of the vocalisation; ⁴: parameters related to the shape of the frequency distribution

249 *Statistical models*

250 All statistics were carried out on R (R Core Team, 2022). Linear mixed effect models [*lmer*
251 function, *lme4* R package (Bates et al., 2014)] were built when tested variables were linear
252 (behavioural and vocal scores, grunt duration) and one binomial generalized mixed effect model was
253 built for binary parameters (occurrence of missed contacts initiated by human during the
254 conditioning). The following subsections describe how models were built for each type of tests. In all
255 models described below, the identity of the replicate ('1' or '2') was used as an interacting fixed
256 factor, since the experiment was run in two identical replicates on two independent groups. The
257 identity of the human ('AH' or 'AV') was used as interacting fixed factor in all models described

258 below, since two experimenters were involved in the positive handling at weaning and in the session
 259 of additional positive contacts of the conditioning (but always the same human was attributed to a
 260 given piglet). The piglet was used as random factor to take into account the within-subject design.
 261 All explanatory variables used in the models and interactions between them were built in respect to
 262 the experimental design and to allow biological interpretations. As a consequence, not all
 263 interactions between all variables were made. They are fully explained in the subsequent sections.

264 **Isolation/Reunion tests**

265 The aim of this part was to test the effect of the positive handling at weaning treatment (H vs. H+
 266 piglets) and additional human contacts during sessions of the conditioning on the piglet's reaction to
 267 human presence. Since the same Isolation/Reunion test was repeated before and after the
 268 conditioning, we used the variable 'Conditioning time' as a two level interacting factor ('before' or
 269 'after' conditioning, referred as "Time" in the models) to test the effect of the conditioning. Piglets
 270 spacial behaviour and proximity to the human was studied only during the reunion phase with the
 271 human that followed the isolation phase. Model_1 was computed:

```
272 Model_1 <- lmer (ReuPCs ~ Treatment*Time + Treatment*Replicate +
273 Treatment*HumanID + Time*Replicate + Time*HumanID + (1 | pigletID), data=
274 data_Behaviour_Reunion).
```

275 Concerning the analysis of vocal behaviour, the isolation phase represents a negative social context
 276 for the piglets and may be used as a negative control when monitoring the effect of human presence
 277 on vocal expression of emotional states (Villain, Lanthony, et al., 2020). So, the two phases of the
 278 test were used to study the three way interaction between treatment (H vs.. H+), phase of the test
 279 (isolation vs.. reunion) and time of the conditioning (before vs.. after). The following model_2 was
 280 computed:

```
281 Model_2 <- lmer (VocPCs ~ Treatment*Phase*Time + Treatment*HumanID + Time*HumanID
282 + Treatment*Replicate + Time*Replicate + (1 | pigletID/Time/Phase) , data=
283 data_Vocal_Isolation + data_Vocal_Reunion).
```

284 To go further, only the reunion phase was kept and a proximity variable was added. Indeed, the
 285 piglet could vocalise either when close to human or away from them and this spatial proximity was
 286 demonstrated as an important factor of changes of vocal features (Villain et al. 2020b). Thus, a two
 287 level proximity factor was built: either '1' when the piglet was in the proximal area (figure 1) or '0'
 288 when it was elsewhere in the room. The following model_3 was computed:

```
289 Model_3 <- lmer (Vocal response score ~ Treatment*Time*InProxArea +
290 Treatment*HumanID + InProxArea*HumanID + Treatment*Replicate +
```

291 InProxArea*Replicate + Time*Replicate + Time*HumanID + (1 | pigletID/Time), data
 292 = data_Vocal_Reunion).

293 **Conditioning trials**

294 The aim was to study the evolution of human-piglet relationship over the conditioning [the variable
 295 ‘Trial number’, used as a continuous variable, referred as “Trial” in the models]. The effect of
 296 treatment (positively handled at weaning H+ piglets or non handled H piglets) was tested as an
 297 interacting factor with Trial. Trial was also used as a random slope to take into account individual
 298 trajectories (Schielzeth and Forstmeier 2009). The following model_4 was built to test the
 299 behavioural response scores CondPCs (lmer) and the occurrence of missed contact initiated by the
 300 human during a session (presence/absence, binomial model, glmer):

```
301 Model_4 <- (g)lmer (CondPCs / Missed contact ~ Trial*Treatment + Trial*HumanID +
302 Trial*Replicate + Treatment*Replicate + Treatment*humanID + (1+ Trial |
303 pigletID), (family=Binomial), data= data_Behaviour_Conditioning).
```

304 For the analysis of vocal response scores, similarly to the Isolation/Reunion test, the piglet could
 305 vocalise either when close to the human or away from them. We thus added the proximity factor in
 306 the analysis of vocal response variables. The following model_5 was built :

```
307 Model_5 <- lmer (VocPCs ~ Trial*Treatment*InProxArea+ Trial*HumanID +
308 Trial*Replicate + Treatment*Replicate + Treatment*HumanID + HumanID*InProxArea +
309 Replicate*InProxArea + (1+ Trial | pigletID), data= data_Vocal_Conditioning).
```

310 **Model validation and statistical tests**

311 All linear models were validated by visual inspection of the symmetrical and normal distribution of
 312 the residuals. Anovas (‘car’ R package (Fox & Weisberg, 2011)) were computed on models to test
 313 for significant effects of explanatory variables. Following the Anova, when interactions were found
 314 significant, post hoc test were run on model interactions, correcting for multiple testing with Tukey
 315 contrasts (‘emmeans’ or ‘lrends’ functions from ‘emmeans’ R package (Lenth, 2016), for
 316 categorical or continuous variables respectively). Considering the conditioning time (before or after
 317 conditioning), when involved in a significant three-way interaction, this factor was fixed to allow
 318 pairwise comparison within each time period as it was not considered relevant to assess the effect of
 319 time only. Results of the Anova, model estimates and pairwise post hoc comparisons are reported in
 320 the supplementary material (tables S1 and S2 for tests, table S3 for model estimates).

321

322 **Results**323 Effect of positive handling at weaning and conditioning on piglets'
324 reaction to human presence (Isolation/Reunion tests)325 ***Piglets that were not handled at weaning express a similar behavioural proximity***
326 ***to a human after a positive conditioning as the positively handled ones.***

327

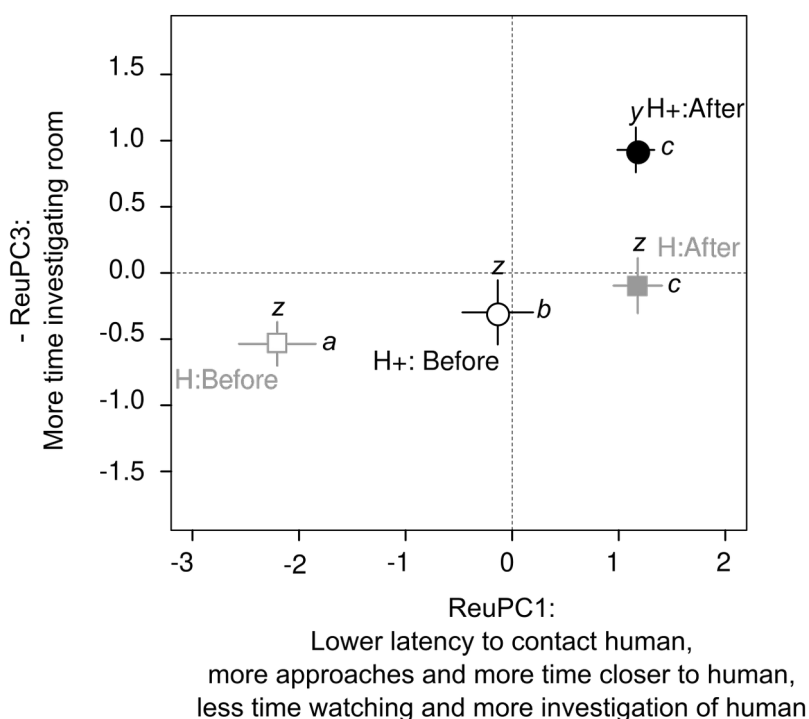


Figure 2: Effect of conditioning and treatment on spatial behaviour and proximity toward the human during the reunion of the Isolation/Reunion test. Mean \pm SE per group is indicated, different letters indicates significantly different groups. Significant interaction between treatment (H : grey squares and H+ : black circles) and time (Before the conditioning: empty elements and After the conditioning: filled elements) on behavioural ReuPC1 (letters a to c) and ReuPC3 (letters z and y). Full statistical report is available as supplementary material (tables S1 S2 for statistical tests and S3 for model estimates)

328 The interaction between the treatment (positively handled piglets at weaning (H+) or not (H) and
329 the conditioning time (before or after the conditioning) was significant for both ReuPC1 and ReuPC3
330 ($\chi^2_1 = 28.0$, $p < 0.001$, and $\chi^2_1 = 3.7$, $p = 0.05$ respectively, figure 2) but not for ReuPC2 ($\chi^2_1 <$
331 0.001 , $p = 0.99$, supplementary table S1). Post hoc tests on ReuPC1 showed that ReuPC1 was higher
332 after the conditioning than before (H: after – before, t.ratio = 12.1, $p < 0.001$, H+: after – before
333 t.ratio = 11.0, $p < 0.001$) and that before the conditioning, piglets that were positively handled at
334 weaning had significantly higher ReuPC1 than non handled piglets (Before, H – H+: t.ratio = -2.1, p
335 < 0.001), but not after (After, H – H+: t.ratio = 0.02, $p = 1.0$). According to the loadings, this means

336 that piglets that were positively handled at weaning had a lower latency to contact the human,
 337 approached them more often and spent more time close to and investigating the human (ReuPC1)
 338 than non handled piglets, before the conditioning. This score increased after the conditioning and no
 339 evidence of a difference between treatments after the conditioning was found (figure 2). Post hoc
 340 tests on ReuPC3 showed a significant effect of the conditioning time only in piglets that were
 341 positively handled at weaning (H+: after – before, t.ratio = 5.2, $p < 0.001$, H: after – before, t.ratio =
 342 2.6, $p = 0.06$). No difference in ReuPC3 was found between treatments before the conditioning
 343 (Before: H – H+, t.ratio = -0.75, $p = 0.87$), whereas positively handled piglets had a higher -ReuPC3
 344 after the conditioning than before (After : H – H+, t.ratio = -3.2, $p = 0.009$). According to the
 345 loadings, this means that after the conditioning, piglets that were positively handled at weaning
 346 expressed more investigation of the room after the conditioning than non handled piglets. No
 347 evidence of any effect on ReuPC2 was found (table S2).

348 ***Piglets positively handled at weaning produce shorter grunts even when no human***
 349 ***is present.***

350 Using the isolation phase as a negative control we could compare the effect of the phase of the test
 351 (Isolation vs. Reunion with the human), taking into account the conditioning time (before or after the
 352 conditioning) and the treatment. No evidence of any effect of neither the three way interaction ($\chi^2_1 <$
 353 0.62, $p > 0.43$) nor two way interactions of interest was found (treatment: phase, conditioning
 354 time:phase, conditioning time: treatment interactions : $\chi^2_1 < 3.5$, $p > 0.06$, table S2) in any of the
 355 scores.

356 Regardless of the treatment, single effects of the phase of the test were significant for grunt
 357 duration and all AcPCs ($\chi^2_1 > 6.6$, $p < 0.01$, table S1). During the reunion phase with the human,
 358 grunts were shorter (estimates of log(duration)[95% CI] : -1.32[-1.37;-1.26] vs. -1.06[-1.12;-1.00]),
 359 had a higher frequency range, higher bandwidth and a higher noise component (-VocPC1:
 360 0.78[0.48;1.08] vs. 0.34[0.03;0.66]), were higher pitched (VocPC2: -0.18[-0.36;0.01] vs. -0.46[-
 361 0.65;-0.28]) and their spectrum had a higher skewness and kurtosis (VocPC3: -0.25[-0.37;-0.14] vs. -
 362 0.11[-0.23;0.01]), compared to the isolation phase.

363 Regardless of the phase of the test, single effects of treatment were found for grunt duration and -
 364 VocPC3 ($\chi^2_1 = 5.5$, $p = 0.02$ and $\chi^2_1 = 4.9$, $p = 0.03$ respectively, table S2). Grunts produced by
 365 positively handled at weaning piglets were shorter (estimates of log(duration)[95% CI]: -1.25[-1.32;-
 366 1.19] vs. -1.12[-1.2;-1.1], table S3), and differed in -VocPC3 scores, describing the shape of the

367 frequency spectrum (estimates of -VocPC3[95% CI]: -0.29[-0.43;-0.14] vs. -0.07[-0.22;0.08], table
 368 S3), than grunts produced by non handled piglets.

369 **Positive handling and conditioning affect vocal reactivity to human proximity.**

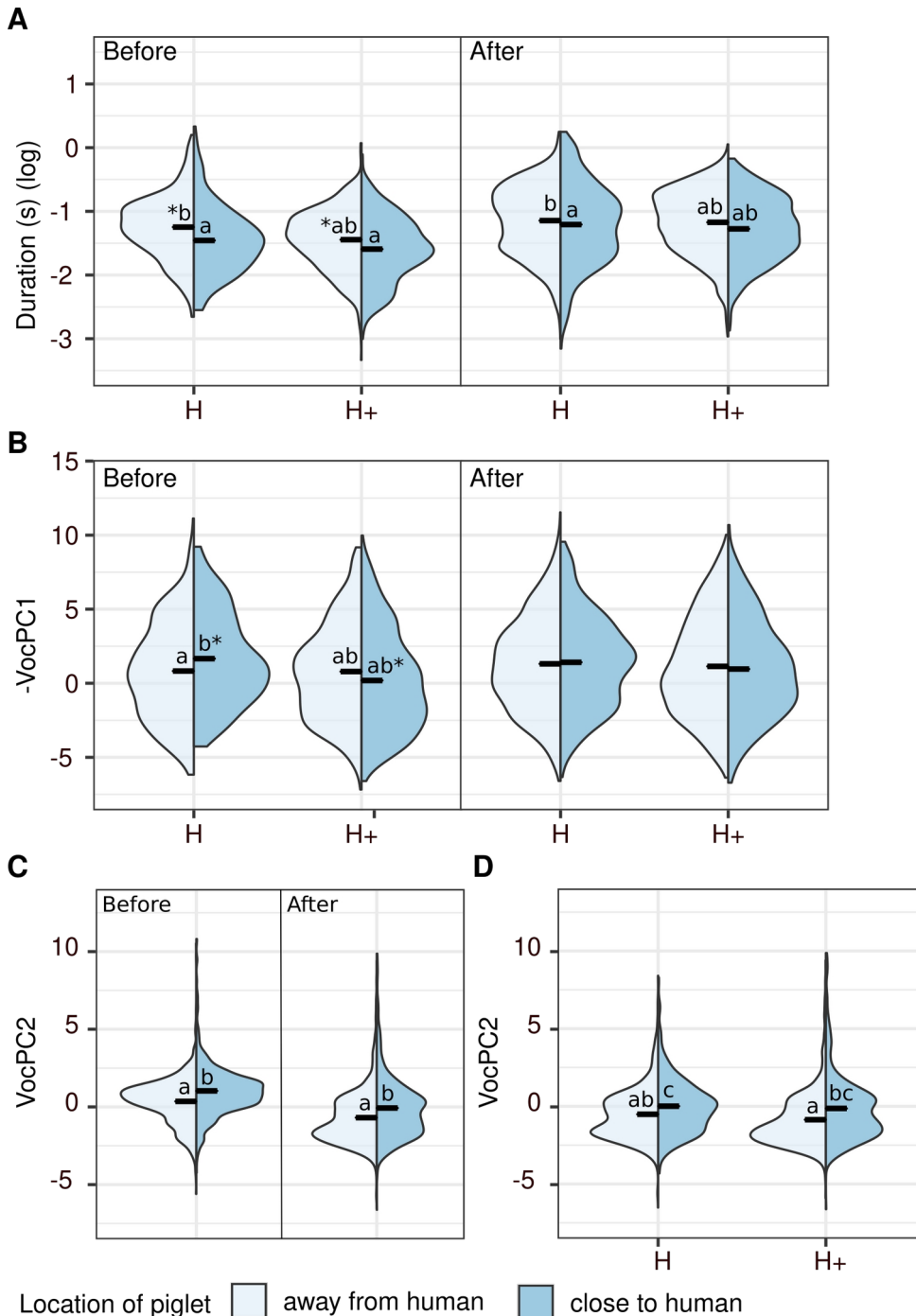


Figure 3: Acoustic structure of grunt during the reunions with a silent and static human (Isolation/Reunion test). Effect of conditioning (before or after), treatment (H or H+) and location of the piglet relatively to the human (close: dark blue or away from them: light blue). Violin plots representing the median and the density of data distribution in the considered groups. (A, B) Results of post hoc tests following significant three way interaction between treatment, conditioning time and location on grunt duration (A) and on the first vocal score -VocPC1 (B). (C,D) Results of post hoc tests following significant two way interactions between conditioning time and location (C) and between treatment and location (D) on the second vocal score VocPC2. Values with no common letters differ significantly. When no letters are present, no significant difference between groups was found. Stars (*) between two groups represent a statistical trend ($p < 0.10$). Full statistical report is available as supplementary material (tables S1 S2 for statistical test and S3 for model estimates).

370 During the 5 min reunion, the piglet was scored either as close to the human or away from them.
371 The three way interaction of the conditioning time, the treatment and the location was significant for
372 grunt duration, -VocPC1 and VocPC3 ($\chi^2_1 > 4.9$, $p < 0.03$). Post hoc tests revealed that grunts
373 produced closer to the human were shorter than the ones produced further away, but only in piglets
374 that were not positively handled at weaning, effect being stronger before the conditioning than after
375 it (H piglets: away – close, $z.ratio = 6.3$, $p < 0.001$ before and $z.ratio = 4.1$ $p < 0.001$ after the
376 conditioning; H+ piglets: away – close $z.ratio < 1.98$ $p > 0.19$, figure 3A). -VocPC1 was higher, i.e.
377 grunts had a higher frequency range, bandwidth and were noisier when produced closer to the human
378 than further away, but only in non handled piglets and before the conditioning (H piglets: away –
379 close, $z.ratio = -3.34$, $p = 0.005$ before and $z.ratio = -1.23$ $p = 0.61$ after the conditioning; H+ piglets:
380 away – close, $z.ratio < 0.36$ $p > 0.21$, figure 3B). For VocPC2, the three way interaction did not
381 reach significance ($\chi^2_1 = 3.3$, $p = 0.07$), so only subsequent two way interactions were considered
382 (post hoc tests on the three way interaction can be found in supplementary, tables S1 to S3). For
383 VocPC2, significant two way interactions were found between the conditioning time and the location
384 ($\chi^2_1 = 10.3$, $p = 0.001$) on the one hand, and between the location and the treatment ($\chi^2_1 = 4.2$, $p =$
385 0.04) on the other hand. Post hoc tests revealed that grunts produced closer to the human had a
386 higher VocPC2, meaning they had a higher pitch, effect being stronger before the conditioning than
387 after (before: away – close, $z.ratio = -6.12$, $p < 0.001$; after: away – close, $z.ratio = -2.88$, $p = 0.004$,
388 figure 3C). The increase in VocPC2 with the location was greater for non handled piglets than
389 positively handled piglets (H piglets: away – close, $z.ratio = -5.54$, $p < 0.001$; H+ piglets: away –
390 close, $z.ratio = -3.82$, $p = 0.001$, figure 3D). The last two-way interaction of interest between the
391 conditioning time and the treatment did not reach significant level ($\chi^2_1 = 0.80$, $p = 0.37$). For
392 VocPC3, post hoc tests did not reach significant levels ($|z.ratio| < 2.3$ $p > 0.09$ for any comparison) .

393

394 Emergence of positive perception of human (effect of additional
 395 positive contacts sessions over the conditioning)

396 ***The conditioning increases behavioural proximity to the human in all piglets.***

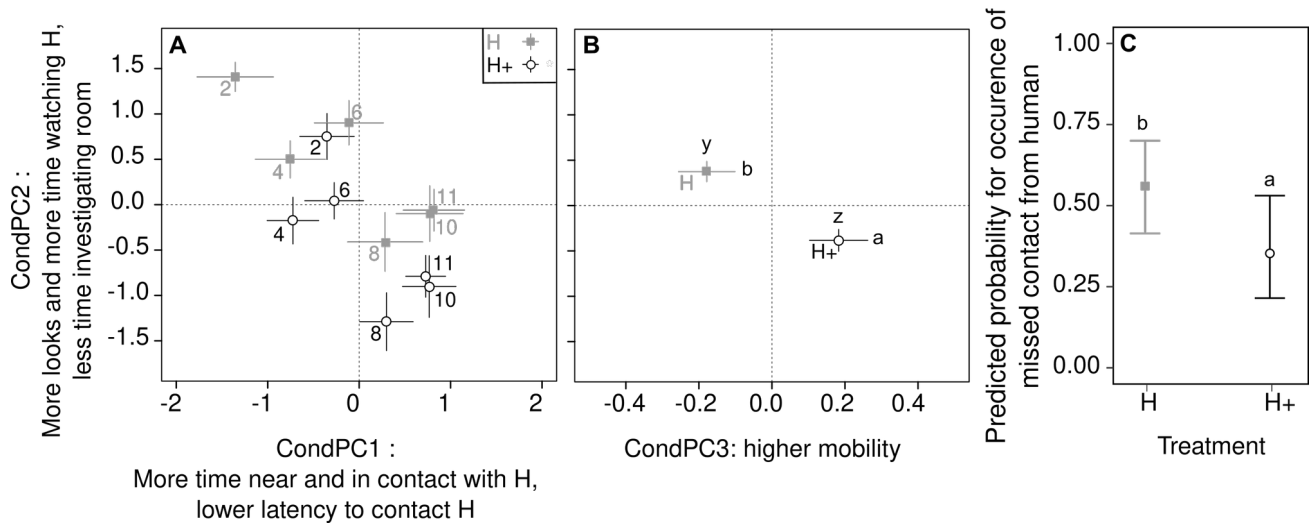


Figure 4: Behavioural variation of responses of piglets according to the sessions of additional positive contacts of the conditioning (A), and to the treatments (B, C). (A,B) Mean \pm SE per group. Numbers in (A) refers to the trial number of the conditioning. Higher CondPC1 and lower CondPC2 over time (single effect of trial number, A). Higher CondPC2 in H piglets than H+ piglets regardless of time (single effect of treatment, A). Higher CondPC3 and lower CondPC2 in H+ piglets than H piglets (single effect of treatment, B). (C) Mean estimates \pm 95% confidence interval from generalized mixed effect model. Lower probability of occurrence of missed contact by the human in H+ than H piglets (single effect of treatment). Full statistical report is available as supplementary material (tables S1 et S2 for statistical tests, table S3 for model estimates).

397 No evidence of any effect of the interaction between the treatment [positively handled piglets
 398 before the conditioning (H+) or not (H)] and the trial number was found for all behavioural scores
 399 (CondPC1, CondPC2 and CondPC3, table 3). Independently from the treatment, the higher the trial
 400 number the higher CondPC1 ($\chi^2_1 = 59.3$, $p < 0.001$, slope estimate [95% confidence interval]: 0.20
 401 [0.15 : 0.25]) and the lower CondPC2 was ($\chi^2_1 = 48.6$, $p < 0.001$, slope estimate: -0.17 [-0.22 : -
 402 0.12]). According to the loadings, over the conditioning, piglets decreased the latency to contact the
 403 human, made more contacts, spent more time in the proximal area and in contact with the human
 404 (condPC1), decreased the number of looks to the human, spent less time watching the human and more
 405 time investigating the room (CondPC2) (figure 4A). Independently from the trial number, positively
 406 handled piglets had a lower CondPC2 and a higher CondPC3 than the non handled ones ($\chi^2_1 = 12.8$,
 407 $p < 0.001$ and $\chi^2_1 = 7.0$, $p = 0.008$ respectively), meaning that piglets that were positively handled at
 408 weaning expressed a fewer number of looks to the human, spent less time watching them and more
 409 time investigating the room (CondPC2) and crossed more virtual zone during the test (CondPC3)
 410 (figure 4B). The probability of having at least one missed contact by the human during a session was

411 lower for positively handled piglets than non handled ones ($\chi^2_1 = 9.57$, $p = 0.002$, figure 4C), with no
 412 interaction with the trial number ($\chi^2_1 = 0.22$, $p = 0.064$).

413 ***Additional positive contacts trigger shorter and higher pitch grunts in all piglets.***

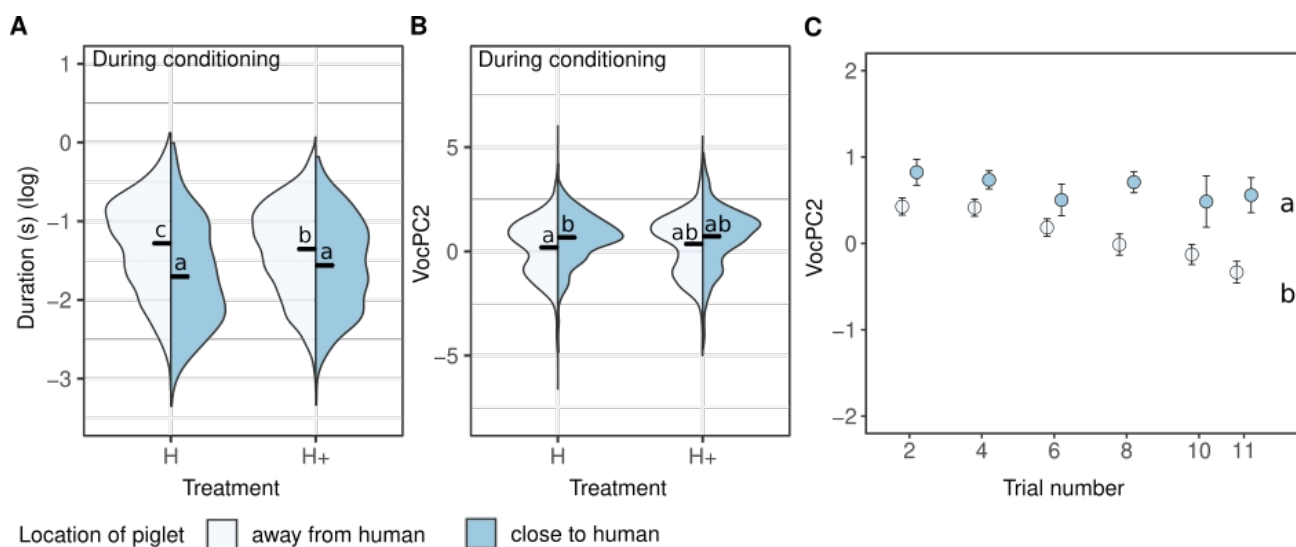


Figure 5: Vocal scores over the conditioning, during the 2min sessions of additional positive contacts. (A, B) Violin plots representing the median and the density of data distribution in the group. Interacting effect of location (in proximal area of the human 'close': dark blue) or elsewhere in the room ('away' from the human: light blue) and treatment (H vs. H+ piglets) on grunt duration (A) and VocPC2 (B). (C) Mean \pm SE per group, interacting effect of trial number and location of piglets on VocPC2. Values with no common letters differ significantly (difference between groups: A, B or slopes: C). Full statistical report is available as supplementary material (tables S1-S3).

414

415 During the sessions of additional positive contacts of the conditioning, the three-way interaction
 416 between the trial number, the treatment and the location was not significant for any of the vocal
 417 scores ($\chi^2_1 < 0.18$, $p > 0.67$), allowing the analysis of the two way interactions of interest. The
 418 interaction between treatment and the trial number was not significant for all vocal scores ($\chi^2_1 < 2.5$
 419 $p > 0.11$). Grunt duration decreased over time and independently from the treatment (trial
 420 number:replicate interaction, $\chi^2_1 < 5.3$ $p = 0.02$, slope estimate $-0.03[-0.04;-0.01]$ for the lower slope,
 421 table S1 and S3). However, independently from the trial number, grunt duration was lower when
 422 piglets were located close to the human and this effect was stronger in non handled piglets than
 423 positively handled piglets (treatment:location interaction: $\chi^2_1 = 15.8$ $p < 0.001$, away vs.. close, H
 424 piglets: z.ratio = 10.2 $p < 0.001$, H+ piglets: z.ratio = 6.86 $p < 0.001$, figure 5A). -VocPC1 and
 425 VocPC2 decreased over time but remained higher when piglets were located close to the human (trial
 426 number: location interaction, $\chi^2_1 = 3.97$ $p = 0.05$ and $\chi^2_1 = 6.1$ $p = 0.01$ respectively for -VocPC1 and
 427 VocPC2). According to the loadings, this means that the frequency range, bandwidth and noisiness
 428 of grunts (-VocPC1) as well as the pitch (VocPC2) decreased over the conditioning when piglets
 429 were located away from the human but remained high when piglets were close (slope comparison

430 away – close, -VocPC1 : z.ratio = -1.80 p = 0.07, VocPC2 : z.ratio = -2.34 p = 0.02, figure 5C).
 431 Additionally, VocPC2 was higher when piglets were close to the human in non handled piglets
 432 (treatment:location interaction, $\chi^2_1 = 7.6$ p = 0.005, pairwise comparisons away vs. close, in H:
 433 z.ratio = -4.9 p < 0.001 and in H+: z.ratio = -2.0 p = 0.21), meaning that non handled piglets
 434 produced higher pitched grunts when closer to the human (figure 5B).

435 Impact of human identity on piglets behaviour and grunt structure

436

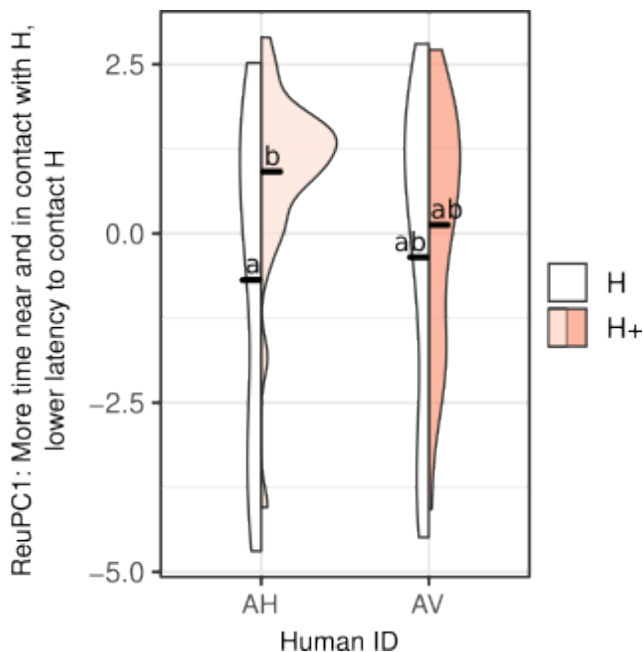


Figure 6: Effect of human identity on spatial behaviour and proximity during the reunion of the Isolation/Reunion test. Violin plots representing the median and the density of data distribution in the group. Values with no common letters differ significantly. Full statistical report is available as supplementary material (tables S1 and S2 for statistical tests, table S3 for model estimates).

437 Since half of the piglets had been assigned to one human experimenter and the other half to another
 438 one, the identity of the human was included in the model. This allowed to test interactions between
 439 the identity of the human and the treatment of positive handling at weaning on the one hand and the
 440 conditioning time on the other hand.

441 During the reunions of the Isolation/Reunion test, the interaction between treatment and human
 442 identity was significant for the first behavioural proximity score (ReuPC1, $\chi^2_1 = 6.01$, p = 0.01) but
 443 not the others (ReuPC2 and ReuPC3 ($\chi^2_1 < 1.98$, p > 0.16, table S1). The effect of treatment on
 444 ReuPC1 was higher when piglets were handled by the human 'AH' (H vs. H+, AH: t.ratio = -4.77, p
 445 < 0.001, figure 6). When the human 'AV' handled the piglets, for which ReuPC1 scores exhibited
 446 intermediate values, treatment was not significant (AV, H vs. H+: t.ratio = -1.33, p = 0.56). These

447 interacting effects of the human identity and treatment on behaviour were not found when
448 considering the reunions of the conditioning ($\chi^2_1 < 1.32$, $p > 0.25$ for all CondPCs, table S1).

449 Interactions between the human identity and conditioning time were not significant, neither
450 considering the reunions of the Isolation/Reunion test (ReuPCs, $\chi^2_1 < 0.642$, $p > 0.42$, tables S1),
451 neither the trial number during the session of additional positive contacts of the conditioning
452 (CondPCs, $\chi^2_1 < 0.11$ $p > 0.74$, table S1).

Table 5: Significant effects of human identity on vocal response score (VocCPI and VocPC2) during the reunion of the Isolation/Reunion test and during the sessions of additional positive contacts of the conditioning. Only significant effect are presented here but a full statistical report is available as supplementary material (tables S1 and S2 for statistical tests, table S3 for model estimates). When single effects were interpretable, the Chi-squared statistic are reported. When significant interactions were significant, post hoc pairwise comparisons were performed with Tukey corrected and are thus reported. The estimates correspond either to the group estimate and comparisons of groups (categorical fixed effect) or slope estimates and comparison of slopes (continuous fixed effect, 'Trial number').

Vocal response score	Fixed effect	Levels	Estimate	Lower.95%CI	Upper.95%CI	Statistic	P-value
Reunion of the Isolation/Reunion test							
VocPC2	humanID	AH	0.154	-0.119	0.427	$\chi^2_1 =$ 4.94	P = 0.03
		AV	-0.292	-0.571	-0.012		
Sessions of additional positive contacts of the conditioning							
-VocPC1	humanID	AH	0.091	0.037	0.144	$\chi^2_1 =$ 4.69	P = 0.03
		AV	0.076	0.021	0.132		
VocPC2	humanID*InProxArea	AH – away	0.317	0.110	0.524	Z-ratio = -1.23	P = 0.60
		AH – close	0.402	0.161	0.643		
		AV – away	0.027	-0.182	0.236	Z-ratio = -5.77	P < 0.001
		AV – close	0.462	0.212	0.712		
VocPC3	humanID * Trial number	AH – Trial number	-0.048	-0.070	-0.026	Z-ratio = -2.82	P = 0.005
		AV – Trial number	-0.007	-0.031	0.016		

453

454 Considering the vocal scores, no effect of human identity was found on VocPC1 during the
455 Isolation/Reunion tests but -VocPC1 was higher when the human 'AH' was in the room during the
456 reunion periods of the conditioning (table 5), meaning the frequency range and the bandwidth of the
457 grunt were higher when the human 'AH' interacted with the piglet compared to the human 'AV'.
458 VocPC2 was higher when the human 'AH' was in the room during the Isolation/Reunion tests (table
459 5), meaning that the pitch of grunts was higher and this effect was also found during the sessions of

460 additional positive contacts of the conditioning in interaction with the location of the piglet ($\chi^2_1 =$
461 11.9, $p = 0.001$): VocPC2 increased when piglets were located close to the human but this increase
462 was significant only for the human 'AV' and not for 'AH' (table 5). VocPC3 was not different
463 between humans during the reunions of the Isolation/Reunion tests but, over the conditioning,
464 VocPC3 changed differently when piglets were handled by the human 'AH' or 'AV', as showed by
465 the significant interaction between trial number and human identity ($\chi^2_1 = 8.0$, $p = 0.005$): the
466 skewness and kurtosis of grunts decreased over the conditioning when 'AH' was interacting with the
467 piglets, but not 'AV' (see slope estimates, table 5). No evidence of any effect of human identity was
468 found on grunt duration neither during the Isolation/Reunion tests nor during the sessions of
469 additional positive contacts of the conditioning (table S1).

470 **Discussion**

471 In this study, familiarity to a human and human-animal interactions were experimentally modified
472 in weaned piglets to study the establishment of a positive HAR and test whether grunt structure could
473 reflect a positive HAR. A positive conditioning paradigm, using additional positive contacts from a
474 human as a reward, allowed to compare the behavioural changes over time in piglets previously
475 positively handled at weaning or not. Two types of sessions were studied: a standard
476 isolation/reunion tests with the human, carried out before and after conditioning, during which the
477 human remained silent and did not interact with the piglet, and sessions of the conditioning, during
478 which the human interacted with the piglets, providing additional positive contacts, as long as the
479 piglets stayed close to the seated human. Behavioural data were collected to describe the positive
480 HAR. Grunts produced during the tests and sessions were collected and their spectro-temporal
481 structure confronted to the behavioural data, with the hypothesis that vocalisation structure may
482 reflect the quality of HAR, though vocal markers of positive emotions. Firstly, the discussion will
483 focus on the behavioural validation of the establishment of a positive HAR. Secondly, behavioural
484 and vocal expression will be confronted to discuss grunt spectro-temporal structure as indicator of
485 the quality of HAR. Last, we will discuss perspectives regarding the effect of human identity on the
486 establishment of a positive HAR.

487 Behavioural evidence of a rapid establishment of interest and 488 proximity toward a human providing additional positive contacts

489 The standard reunion test with the human before the conditioning showed first that the treatment of
490 positive handling at weaning succeeded in creating two different levels of human-piglet relationship

491 (H and H+), as positively handled piglets expressed a higher attraction toward the human than non
492 handled piglets (ReuPC1), parameters considered as indicators of a positive HAR (Rault et al.,
493 2020). Second, this test showed that the conditioning increased the behavioural proximity toward the
494 human of both positively handled and non handled piglets so that non handled piglets expressed a
495 similar attraction toward the human as positively handled piglets. These results are in line with the
496 behavioural results of the sessions of additional positive contacts. The analysis of piglets' behaviour
497 every second sessions of the conditioning showed that, although positively handled and non handled
498 piglets started with different degree of proximity toward the human (trials 2 and 4, CondPC1), then,
499 over time and for both treatments (H and H+), piglets expressed a higher attraction toward the human
500 (CondPC1) and avoided less the human when the latter attempted to interact with them. So it seems
501 that the conditioning process allowed non handled piglets to compensate the lack of positive
502 handling before the conditioning and develop a similar proximity toward the human. Two minute
503 daily sessions of additional positive contacts changed positively the perception of the human for the
504 piglets, and thus their willingness to interact with them. Since no evidence of any interaction
505 between time and treatment was found, no conclusion on differential developmental trajectories
506 between treatments can be drawn, but a parallel development of the human-piglet relationship in
507 both groups, when considering the proximity.

508 Beside behavioural proximity, piglets that were positively handled at weaning expressed more
509 exploratory behaviours than non handled piglets after the conditioning (ReuPC3). This was also
510 observed during the sessions of additional positive contacts of the conditioning: positive handled
511 piglets started with a higher score associated with investigation than non handled piglets (CondPC2)
512 and it held over the conditioning. Piglets that were positively handled at weaning also expressed a
513 higher mobility than non handled piglets (CondPC3). These observations may be interpreted as an
514 expression of natural foraging and disinterest from human contact, which may be a sign of positive
515 welfare (Weerd & Day, 2009). In addition, this could also be interpreted in terms of attachment to
516 the human. Indeed, attachment to a human may facilitate exploration of novel environments or
517 objects, as shown in dogs (Palmer & Custance, 2008). A period of positive handling at weaning may
518 provide an environment secure enough for the piglets to explore their environment in the presence of
519 the human. Attachment has also been hypothesised in the lambs-human relationship (Tallet et al.,
520 2009).

521 Overall, the behavioural monitoring showed that 2 min sessions of positive additional contacts per
522 day are sufficient to increase proximity to a human to similar levels as when piglets were previously

523 familiarised for 2 weeks, even when piglets experienced social isolation. But it did not allow the non
524 handled piglets to express natural exploratory behaviours as the positively handled piglets. We
525 hypothesize a sequential establishment of a positive HAR over time: firstly with a decrease of
526 attentive state and an increase in proximity and accepted contacts, and secondly with a disinterest of
527 human contacts and the expression of natural foraging behaviour. The latter may require a higher
528 exposure time.

529 In the next paragraph we discuss to what extent changes in grunt spectro-temporal structure may
530 reflect behavioural changes linked to the positive HAR over time.

531 Links between vocal expression and positive HAR

532 *A positive HAR is reflected by shorter grunts in presence and absence of a human*

533 The social isolation phase of the Isolation /Reunion test, before any human entered the room, was
534 associated with longer, lower pitched grunts with a downshifted frequency spectrum, whereas the
535 reunion with a static human changed grunts structure to shorter, higher pitched with an upshifted
536 frequency spectrum and this was observed in both handled and non handled piglets (H or H+) as well
537 as before and after the conditioning. In terms of emotional indicators, similar changes in acoustic
538 features of grunts were found in studies focusing on vocal markers of valence in pigs (Briefer et al.,
539 2019, 2022; Friel et al., 2019; Villain, Hazard, et al., 2020), meaning that the reunion with a human,
540 after a period of social isolation would be perceived as positive. However, this modulation of grunt
541 structure was observed regardless of piglet experience with the human. It is possible that the reunion
542 with an either neutral or familiar human, releasing piglets from total isolation could be perceived as
543 positive by the piglets, as suggested in previous studies (Villain, Lanthony, et al., 2020).

544 In addition, and surprisingly, positively handled piglets produced shorter grunts than non handled
545 piglets regardless of human presence. This was previously shown in another context (anticipation of
546 (pseudo)social events independently from the type of partner) in the same groups of piglets (Villain,
547 Hazard, et al., 2020). This may show that the period of positive handling at weaning modulated vocal
548 expression in the long term, as this result was found both before and after the conditioning. On the
549 one hand, a positive HAR establishes through successive positive experiences (Rault et al. 2020)
550 and, on the other hand, HAR may have long term effects on behavioural expressions, as suggested by
551 Brajon et al. (2015) using cognitive bias tests. We can thus hypothesize this may also be reflected in
552 the way piglets vocalise, in general. In that case, we may have evidence of expression of another

553 category of affect, moods, and not only emotional expression. Indeed, as suggested by Schnall
554 (2010), although emotions are short-term affects triggered by an external stimulus, moods, on the
555 other hand, may be experienced on a longer term and may not be attributable to a specific stimulus.
556 Although emotions and moods do not rely on the same time scale, they may interact with one
557 another, and more studies are needed to understand their effects on vocal expression.

558 *A positive HAR affects vocal reactivity toward a static human*

559 In a previous study, we showed that pigs vocalizing close to a human that previously had provided
560 repetitive additional positive contacts produced shorter and higher pitch grunts, compared to when
561 vocalizing away from the human (Villain, Lanthony, et al., 2020). Using the same type of test with
562 positively handled at weaning and non handled piglets, before or after conditioning sessions with
563 positive interactions, we can test the effect of positive handling on this modulation of grunt structure.
564 Similarly to the previous study, during the standard reunion test (no contact from the human), piglets
565 produced shorter and higher pitched grunts with an upshifted frequency spectrum when close to the
566 human. It has to be noted that this effect was 1) stronger in previously non handled piglets than
567 positively handled at weaning piglets and 2) stronger before the conditioning than after. In other
568 words, the more familiar with the human associated with positive handling, the less reactive to
569 human proximity.

570 These results may be interpreted according to the behavioural results we described earlier (fig. 2).
571 We described that the proximity to the human was first increasing at the beginning of positive
572 handling experiences (see H piglets, before vs. after conditioning) before reaching a maximum (see
573 H vs. H+ piglets after conditioning) and that the most familiar piglets showed more exploratory
574 behaviours (H+ after conditioning). The acoustic results during the standard reunion mirror the
575 behavioural results from the same test. The least familiar piglets would vocally express the
576 exploration of a neutral and static human and, as the familiarity with the human increases, the human
577 may become part of their environment, explaining the lack of vocal reactivity when close to the static
578 human.

579 In addition, we may also be facing ceiling effects in terms of vocal flexibility, which could also
580 partly explain these results. We showed that positively handled piglets generally produce shorter
581 grunts than non handled piglets, and that the shape of the frequency spectrum of these grunts was
582 different. So the structure of their calls, in general is different. According to the source-filter theory
583 of vocal production, vocal flexibility is constrained by the dimensions and functioning of the vocal

584 apparatus (lung capacity, characteristics of the vocal folds, length and shape of the vocal tract, see
585 (Taylor & Reby, 2010) and (Titze & Martin, 1998)). It is possible that the positive HAR developed
586 by the positively handled piglets may have change their grunts structure to an extent that vocal
587 flexibility is no longer quantifiable in the experimental design of this study.

588 ***Providing rewarding additional positive contacts triggers short and high pitched***
589 ***grunts***

590 Contrary to the standard reunions with a static human, the human actively interacted with the
591 piglets during the sessions of the conditioning, providing contacts and producing speech as long as
592 the piglets remained close to the human. During these sessions and contrary to the standard reunions,
593 grunts produced close to the human were shorter and higher pitched, regardless of the trial number of
594 the conditioning and treatment. Although these effects were stronger in non handled piglets than
595 positively handled piglets, they remained over time. We describe here two types of vocal reaction to
596 human proximity, depending on the human behaviour. On the one hand, time decreased vocal
597 reactivity to human proximity during a standard reunion with a static human. On the other hand, no
598 evidence of a decrease in vocal reactivity to human proximity was found during sessions of
599 additional positive contacts. This would mean that positive interactions with piglets consistently
600 triggers the production of shorter and higher pitch grunts. These changes may be explained by the
601 expression of a higher arousal state experienced by the piglets while being positively handled.
602 Indeed, in the context of these sessions, the piglet could choose to approach and stay close to the
603 human, which will provide positive contacts systematically. So the piglet may anticipate to receive
604 positive contact and systematically being rewarded. When close to the human, observed changes in
605 frequency distribution of grunts (increased pitch and upshifted frequency spectrum) are known to be
606 markers of arousal (in the negative state in multiple mamalian species (Briefer, 2012, 2020) and pigs
607 (Linhart et al., 2015)). In addition, these spectral changes were also associated with shorter grunts.
608 Although the duration of grunts is associated with the valence of a situation, the duration may also be
609 an indicator of positive arousal. This hypothesis has to be taken precociously since no additional
610 control of arousal could be done in the present study.

611 This working hypothesis may explain the decrease in vocal reactivity to human proximity observed
612 during the standard reunion test as the HAR becomes more positive. Indeed, before the sessions of
613 the conditioning, positively handled piglets were habituated to a human interacting positively when
614 present whereas non handled piglets were not, hence, during the first standard reunion test, when the
615 human is present but do not interact with the piglet, positively handled and non handled piglets may

616 have diverging expectations regarding the presence of the static and silent human. As positively
617 handled piglets received positive contacts every time they were in the presence of the human, they
618 may have expected positive contacts when approaching and experienced an absence of reward during
619 the test. This has already been hypothesised in piglets deprived from human voice during interactions
620 after a period of habituation to it (Bensoussan et al. 2020). On the contrary, piglets that were not
621 positively handled at weaning never experienced additional positive contacts and being close to a
622 human, having the possibility to investigate them may be some kind of reward after the period of
623 total isolation. After the conditioning, piglets from both treatments were conditioned to receive
624 additional positive contacts and both groups had experienced a first standard reunion test, so they
625 may both experience an absence of reward during the test, which may explain a lower reaction to
626 human proximity, and thus fewer changes on grunt spectro-temporal features.

627 Last, we can raise the question whether changes in grunt structure in reaction to rewarding positive
628 contacts may also be associated with a specific human-pig communication. In other domestic
629 species, owner directed vocalisations has been shown (in cats, reviewed in (Turner, 2017); in dogs
630 (Gaunet et al., 2022)). In addition, studies have found similar socio-communicative behaviours
631 toward a human in socialized pigs and dogs (Gerencsér et al., 2019). Hence, we may profit from
632 testing the existence of human directed vocalisations in pigs, as consequences of their socio
633 communicative abilities.

634 Effect of human identity on piglets' perception: perspectives on 635 HAR

636 We found that the identity of the human had effects on behavioural and vocal response scores.
637 Piglets that were handled by the human 'AH' had higher values of behavioural proximity (ReuPC1)
638 than piglets handled by the human 'AV' during reunion test after a period of isolation. This effect
639 was not found during conditioning sessions. The effect of the human did not interact with the
640 conditioning time, leading to the conclusion that the difference between the two experimenters may
641 have established during the period of positive handling at weaning, prior to the conditioning.
642 Additionally, when the human 'AH' was in the room, piglets produced grunts with a more upshifted
643 frequency spectrum and a higher pitch than when the human 'AV' was in the room. If upshifted
644 grunts may be a indicator of positive higher arousal, then we may conclude that 'AH' was more
645 likely to trigger higher positive states than 'AV'. Interestingly, the human identity and the spatial
646 proximity had different effects on piglets grunts during sessions of additional positive contacts but
647 not when the human was static during the standard reunion test. Hence, it is possible that the way one

648 human interacts (behavioural and vocally) with a piglet may be more or less effective at triggering
649 positive emotions and thus modifications of grunt structure. Several evidence exists in the literature
650 that pigs discriminate humans visual and auditory cues (Bensoussan et al., 2019; Brajon et al.,
651 2015c). Pigs may also show behavioural changes hearing human voice (Bensoussan et al., 2020). We
652 may question the efficiency of different human features to generate a positive HAR. In our study,
653 both humans that interacted with the piglets wear exactly the same clothes and standardized their
654 tactile interactions toward the piglets before starting the study, and agreed on the rhythm and types of
655 sounds (words, intonation) to use, to minimise generating variability although no systematic controls
656 of the human behaviour or spectral feature of voices were performed here. It thus remains unclear
657 whether experimenters interacted differently or if they were initially perceived differently by piglets.
658 Our results show that the identity of the human may modulate piglet proximity and vocal behaviour
659 but the design of this experiment does not allow to find the causes of these observations (behaviour,
660 voice characteristics, or even odour profile). Thus, more studies of human features that are most
661 likely to generate a positive HAR are needed and may be of interest regarding animal welfare. In
662 addition, studying human-piglet relationship in a more systematic way, as in other domestic species,
663 for example the play behaviour in dogs (Horowitz & Hecht, 2016) or the pet directed speech
664 (Jeannin et al., 2017; Lansade et al., 2021), may shed light on the evolution and converging strategies
665 of interspecific relationships. However, the influence of human identity did not modify the general
666 outcomes of our study, but only decreased some effects, suggesting that this variability does not
667 modify the main results, but should be considered in future studies.

668

669 To conclude, we showed that degrees of familiarity toward a human could be reflected in the way
670 piglets vocalise in their presence, and out of it. We also showed that the spatial proximity toward a
671 human providing additional care could change the acoustic structure of piglet grunts. These changes
672 are likely to be linked to positive and more intense emotional states than when piglets are further
673 away from the human. However, it is still unclear whether the changes in grunt structure could also
674 be linked to human-animal communication and more studies are needed to determine it. We did also
675 show that the identity of the human may be of importance, and may generate vocal changes during
676 additional positive contacts that were not associated with changes in behaviour of the human. More
677 systematic studies of human behaviour along with pig behaviour during the human-animal
678 interactions would be needed to have a better understanding of the evolution of HAR, especially
679 interactive interspecific communication as well as providing new procedures to promote positive

680 welfare. We suggest that analysing vocalisations structure may be a good tool to assess the quality of
681 human-pig relationship and help monitor the establishment of a positive HAR.

682 **Authors contributions**

683 Conceived and designed the experiment (A.V., C.T., C.N.). Performed the experiment (A.V., C.G.).
684 Collection and processing of the acoustic and behavioural data (A.V., C.G.). Statistical analyses
685 (A.V.). Contributed to the writing of the manuscript (A.V., C.T., C.N.).

686 **Acknowledgments**

687 We acknowledge all the technical staff at UEPR: especially Patrick Touanel and Marie-Hélène
688 Lohat, who largely participated in handling the piglets. We thank Eric Siroux who helped building
689 the acoustic chamber at the beginning of the experiment, Remi Resmond for great discussions about
690 statistics and Bliss Elizabeth Bagnato-Conlin for their carefully proof reading of the manuscript. All
691 the authors acknowledge Camille Noûs, affirming the collective and open character of the creation
692 and dissemination of knowledge (Cogitamus Laboratory <https://www.cogitamus.fr/indexen.html>).
693 This project is part of the SoundWel project in the framework of the Anihwa Eranet and funded by
694 ANR 30001199.

695 **Data availability**

696 The datasets used for the study are available at (Villain et al., 2022). The folder contains all datasets
697 and a readme to match the type of analysis to the proper dataset. We have made sure to report in the
698 main text of the article which R libraries and which functions in these libraries we used. All formulas
699 of the statistical models are explicit in the text to facilitate transfer of information and replicate the
700 analysis. All libraries are open source as well.

701 **References**

- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting Linear Mixed-Effects Models using lme4. *ArXiv:1406.5823 [Stat]*. <http://arxiv.org/abs/1406.5823>
- Bensoussan, S., Tigeot, R., Lemasson, A., Meunier-Salaün, M.-C., & Tallet, C. (2019). Domestic piglets (*Sus scrofa domestica*) are attentive to human voice and able to discriminate some prosodic features. *Applied Animal Behaviour Science*, *210*, 38–45.
<https://doi.org/10.1016/j.applanim.2018.10.009>
- Bensoussan, S., Tigeot, R., Meunier-Salaün, M.-C., & Tallet, C. (2020). Broadcasting human voice to piglets (*Sus scrofa domestica*) modifies their behavioural reaction to human presence in the home pen and in arena tests. *Applied Animal Behaviour Science*, *225*, 104965.
<https://doi.org/10.1016/j.applanim.2020.104965>
- Boersma & Paul. (2001). Praat, a system for doing phonetics by computer. *Glott International*, *5*(9), 341–345.
- Boivin, X., Tournadre, H., & Le Neindre, P. (2000). Hand-feeding and gentling influence early-weaned lambs' attachment responses to their stockperson. *Journal of Animal Science*, *78*(4), 879–884. <https://doi.org/10.2527/2000.784879x>
- Brajon, S., Laforest, J.-P., Bergeron, R., Tallet, C., & Devillers, N. (2015c). The perception of humans by piglets: Recognition of familiar handlers and generalisation to unfamiliar humans. *Animal Cognition*, *18*(6), 1299–1316. <https://doi.org/10.1007/s10071-015-0900-2>
- Brajon, S., Laforest, J.-P., Schmitt, O., & Devillers, N. (2015b). The Way Humans Behave Modulates the Emotional State of Piglets. *PLOS ONE*, *10*(8), e0133408.
<https://doi.org/10.1371/journal.pone.0133408>
- Briefer, E. F. (2012). Vocal expression of emotions in mammals: Mechanisms of production and evidence. *Journal of Zoology*, *288*(1), 1–20. <https://doi.org/10.1111/j.1469-7998.2012.00920.x>
- Briefer, E. F. (2020). Coding for 'Dynamic' Information: Vocal Expression of Emotional Arousal and Valence in Non-human Animals. In T. Aubin & N. Mathevon (Eds.), *Coding Strategies*

in *Vertebrate Acoustic Communication* (pp. 137–162). Springer International Publishing.
https://doi.org/10.1007/978-3-030-39200-0_6

- Briefer, E. F., Sypherd, C. C.-R., Linhart, P., Leliveld, L. M. C., Padilla de la Torre, M., Read, E. R., Guérin, C., Deiss, V., Monestier, C., Rasmussen, J. H., Špinka, M., Döpjan, S., Boissy, A., Janczak, A. M., Hillmann, E., & Tallet, C. (2022). Classification of pig calls produced from birth to slaughter according to their emotional valence and context of production. *Scientific Reports*, *12*(1), Article 1. <https://doi.org/10.1038/s41598-022-07174-8>
- Briefer, E. F., Vizier, E., Gygax, L., & Hillmann, E. (2019). Expression of emotional valence in pig closed-mouth grunts: Involvement of both source- and filter-related parameters. *The Journal of the Acoustical Society of America*, *145*(5), 2895–2908. <https://doi.org/10.1121/1.5100612>
- Broom, D. M. (2011). A history of animal welfare science. *Acta Biotheoretica*, *59*(2), 121–137. <https://doi.org/10.1007/s10441-011-9123-3>
- Brown, S. L., & Bradshaw, J. W. S. (2014). Communication in the domestic cat: Within- and between-species. In P. P. G. Bateson (Ed.), *The domestic cat: The biology of its behaviour* (Third edition). Cambridge University Press.
- Dray, S., & Dufour, A.-B. (2007). The ade4 Package: Implementing the Duality Diagram for Ecologists. *Journal of Statistical Software*, *22*, 1–20. <https://doi.org/10.18637/jss.v022.i04>
- Fox, J., & Weisberg, S. (2011). *car-package: Companion to Applied Regression*. GitHub. <https://rdr.io/github/jonathon-love/car/man/car-package.html>
- Friel, M., Kunc, H. P., Griffin, K., Asher, L., & Collins, L. M. (2019). Positive and negative contexts predict duration of pig vocalisations. *Scientific Reports*, *9*(1), Article 1. <https://doi.org/10.1038/s41598-019-38514-w>
- Gácsi, M., Györi, B., Miklósi, Á., Virányi, Z., Kubinyi, E., Topál, J., & Csányi, V. (2005). Species-specific differences and similarities in the behavior of hand-raised dog and wolf pups in social situations with humans. *Developmental Psychobiology*, *47*(2), 111–122. <https://doi.org/10.1002/dev.20082>
- Gaunet, F., Savalli, C., & Legou, T. (2022). An exploratory study on dogs' vocalizations towards their owner and food in an unsolvable task. *Applied Animal Behaviour Science*, *246*, 105529. <https://doi.org/10.1016/j.applanim.2021.105529>

- Gerencsér, L., Pérez Fraga, P., Lovas, M., Újváry, D., & Andics, A. (2019). Comparing interspecific socio-communicative skills of socialized juvenile dogs and miniature pigs. *Animal Cognition*, 22(6), 917–929. <https://doi.org/10.1007/s10071-019-01284-z>
- Horowitz, A., & Hecht, J. (2016). Examining dog–human play: The characteristics, affect, and vocalizations of a unique interspecific interaction. *Animal Cognition*, 19(4), 779–788. <https://doi.org/10.1007/s10071-016-0976-3>
- Jeannin, S., Gilbert, C., Amy, M., & Leboucher, G. (2017). Pet-directed speech draws adult dogs' attention more efficiently than Adult-directed speech. *Scientific Reports*, 7(1), Article 1. <https://doi.org/10.1038/s41598-017-04671-z>
- Jerolmack, C. (2009). Humans, Animals, and Play: Theorizing Interaction When Intersubjectivity is Problematic. *Sociological Theory*, 27(4), 371–389. <https://doi.org/10.1111/j.1467-9558.2009.01353.x>
- Kiley, M. (1972). The Vocalizations of Ungulates, their Causation and Function. *Zeitschrift Für Tierpsychologie*, 31(2), 171–222. <https://doi.org/10.1111/j.1439-0310.1972.tb01764.x>
- Lansade, L., Trösch, M., Parias, C., Blanchard, A., Gorosurreta, E., & Calandreau, L. (2021). Horses are sensitive to baby talk: Pet-directed speech facilitates communication with humans in a pointing task and during grooming. *Animal Cognition*, 24(5), 999–1006. <https://doi.org/10.1007/s10071-021-01487-3>
- Laurijs, K. A., Briefer, E. F., Reimert, I., & Webb, L. E. (2021). Vocalisations in farm animals: A step towards positive welfare assessment. *Applied Animal Behaviour Science*, 236, 105264. <https://doi.org/10.1016/j.applanim.2021.105264>
- Lenth, R. V. (2016). *Least-Squares Means: The R Package lsmeans*. 69(1), 1–33. <https://doi.org/doi:10.18637/jss.v069.i01>
- Linhart, P., Ratcliffe, V. F., Reby, D., & Špinka, M. (2015). Expression of Emotional Arousal in Two Different Piglet Call Types. *PLOS ONE*, 10(8), e0135414. <https://doi.org/10.1371/journal.pone.0135414>
- Marx, G., Horn, T., Thielebein, J., Knubel, B., & von Borell, E. (2003). Analysis of pain-related vocalization in young pigs. *Journal of Sound and Vibration*, 266(3), 687–698. [https://doi.org/10.1016/S0022-460X\(03\)00594-7](https://doi.org/10.1016/S0022-460X(03)00594-7)

- McGregor, P. K. (1992). Quantifying Responses to Playback: One, Many, or Composite Multivariate Measures? In P. K. McGregor (Ed.), *Playback and Studies of Animal Communication* (pp. 79–96). Springer US. http://link.springer.com/chapter/10.1007/978-1-4757-6203-7_6
- Mignon-Grasteau, S., Boissy, A., Bouix, J., Faure, J.-M., Fisher, A. D., Hinch, G. N., Jensen, P., Le Neindre, P., Mormède, P., Prunet, P., Vandeputte, M., & Beaumont, C. (2005). Genetics of adaptation and domestication in livestock. *Livestock Production Science*, *93*(1), 3–14. <https://doi.org/10.1016/j.livprodsci.2004.11.001>
- Palmer, R., & Custance, D. (2008). A counterbalanced version of Ainsworth’s Strange Situation Procedure reveals secure-base effects in dog–human relationships. *Applied Animal Behaviour Science*, *109*(2), 306–319. <https://doi.org/10.1016/j.applanim.2007.04.002>
- Peterson, V., Simonsen, H. B., & Lawson, L. G. (1995). The effect of environmental stimulation on the development of behavior in pigs. *Applied Animal Behaviour Science*, *45*(3–4), 215–224. [https://doi.org/10.1016/0168-1591\(95\)00631-2](https://doi.org/10.1016/0168-1591(95)00631-2)
- Puppe, B., Schön, P. C., Tuchscherer, A., & Manteuffel, G. (2005). Castration-induced vocalisation in domestic piglets, *Sus scrofa*: Complex and specific alterations of the vocal quality. *Applied Animal Behaviour Science*, *95*(1), 67–78. <https://doi.org/10.1016/j.applanim.2005.05.001>
- R Core Team. (2022). *R: A language and environment for statistical computing*. (3.1.1). R Foundation for Statistical Computing. <http://www.R-project.org/>.
- Rault, J.-L., Truong, S., Hemsworth, L., Le Chevoir, M., Bauquier, S., & Lai, A. (2019). Gentle abdominal stroking (‘belly rubbing’) of pigs by a human reduces EEG total power and increases EEG frequencies. *Behavioural Brain Research*, *374*, 111892. <https://doi.org/10.1016/j.bbr.2019.04.006>
- Rault, J.-L., Waiblinger, S., Boivin, X., & Hemsworth, P. (2020). The Power of a Positive Human–Animal Relationship for Animal Welfare. *Frontiers in Veterinary Science*, *7*. <https://www.frontiersin.org/article/10.3389/fvets.2020.590867>
- Schmied, C., Boivin, X., & Waiblinger, S. (2008). Stroking Different Body Regions of Dairy Cows: Effects on Avoidance and Approach Behavior Toward Humans. *Journal of Dairy Science*, *91*(2), 596–605. <https://doi.org/10.3168/jds.2007-0360>
- Sueur, J., Aubin, T., & Simonis, C. (2008). Seewave, a free modular too for sound analysis ans

synthesis. *Bioacoustics*, *18*(2), 213–226. <https://doi.org/10.1080/09524622.2008.9753600>

Tallet, C., Linhart, P., Policht, R., Hammerschmidt, K., Šimeček, P., Kratinova, P., & Špinka, M. (2013). Encoding of Situations in the Vocal Repertoire of Piglets (*Sus scrofa*): A Comparison of Discrete and Graded Classifications. *PLOS ONE*, *8*(8), e71841. <https://doi.org/10.1371/journal.pone.0071841>

Tallet, C., Sy, K., Prunier, A., Nowak, R., Boissy, A., & Boivin, X. (2014). Behavioural and physiological reactions of piglets to gentle tactile interactions vary according to their previous experience with humans. *Livestock Science*, *167*, 331–341. <https://doi.org/10.1016/j.livsci.2014.06.025>

Tallet, C., Veissier, I., & Boivin, X. (2009). How does the method used to feed lambs modulate their affinity to their human caregiver? *Applied Animal Behaviour Science*, *119*(1), 56–65. <https://doi.org/10.1016/j.applanim.2009.03.012>

Taylor, A. M., & Reby, D. (2010). The contribution of source–filter theory to mammal vocal communication research. *Journal of Zoology*, *280*(3), 221–236. <https://doi.org/10.1111/j.1469-7998.2009.00661.x>

Titze, I. R., & Martin, D. W. (1998). Principles of Voice Production. *The Journal of the Acoustical Society of America*, *104*(3), 1148–1148. <https://doi.org/10.1121/1.424266>

Turner, D. C. (2017). A review of over three decades of research on cat-human and human-cat interactions and relationships. *Behavioural Processes*, *141*, 297–304. <https://doi.org/10.1016/j.beproc.2017.01.008>

Villain, A. S., Guérin, C., Noûs, C., & Tallet, C. (2022). *The use of pig vocalization structure to assess the quality of human-pig relationship*. Portail Data INRAE, V1. <https://doi.org/10.15454/RTBO3O>

Villain, A. S., Hazard, A., Danglot, M., Guérin, C., Boissy, A., & Tallet, C. (2020). Piglets vocally express the anticipation of pseudo-social contexts in their grunts. *Scientific Reports*, *10*(1), Article 1. <https://doi.org/10.1038/s41598-020-75378-x>

Villain, A. S., Lanthony, M., Guérin, C., & Tallet, C. (2020). Manipulable Object and Human Contact: Preference and Modulation of Emotional States in Weaned Pigs. *Frontiers in Veterinary Science*, *7*, 577433. <https://doi.org/10.3389/fvets.2020.577433>

- Weary, D. M., Braithwaite, L. A., & Fraser, D. (1998). Vocal response to pain in piglets. *Applied Animal Behaviour Science*, *56*(2), 161–172. [https://doi.org/10.1016/S0168-1591\(97\)00092-0](https://doi.org/10.1016/S0168-1591(97)00092-0)
- Weerd, H. A. van de, & Day, J. E. L. (2009). *A review of environmental enrichment for pigs housed in intensive housing systems*. <https://doi.org/10.1016/j.applanim.2008.08.001>