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Title: The use of pigs vocalisation structure to assess the quality of human-pig relationship

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Key words:

Taming, Acoustic communication, Emotions, Mood, Behaviour, Welfare, Interspecific interactions.

Abstract:

In domestic species, studying human-animal interactions and their consequences on the establishment of a positive Human-Animal Relationship (HAR) would have applications for both improving animal welfare. Objectify the quality of a HAR requires information on several aspects of the animal biology and emotional states (spatial behaviour, physiological and cognitive states). Growing evidence show that acoustic features of animal vocalisations may be a indicators of emotional states. Here, we tested the hypothesis that the quality of vocal expression may indicate the quality of HAR. Thirty piglets were tamed thanks to regular interactions with an experimenter talking and physically interacting with them, three times a day from weaning; while 30 other piglets received only contact necessary for their good breeding. Two weeks later, we recorded behaviours and vocalisations produced in presence of the static experimenter for five minutes. The test was repeated two weeks later, after a period of conditioning using human presence and contacts as a reward for all piglets, supposed to lead to a positive human-piglet relationship for all piglets. As expected, taming led to an attraction toward the experimenter, and, after the conditioning, untamed piglets expressed a similar level of attraction than previously tamed piglets. Tamed piglets generally

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produced shorter grunts than untamed piglets. However untamed piglets expressed more flexibility in call structure when vocalising close to a human, with a decrease of grunt duration and an increase of pitch, frequency range and noisiness in their grunt. This differential effect of proximity in tamed and untamed piglets was attenuated after the conditioning during a standard reunion with a static human but remained over time when the human was providing additional positive contacts. Results suggest that first, changes in vocal structure are consistent with indicators of positive states in the presence of a human. Second,increasing familiarity and proximity between a human and a piglet may induce changes in the acoustic structure of their grunts. Third, a carrying human trigger more changes in vocalisation structure than by their presence only. We show that vocalisation structure may allow to assess the quality of human-pig relationship.

Introduction

The long process of domestication has conducted to shape physiology and morphology of domestic animal species, but also their behaviour. It notably has shaped interspecific interactions between human and non human animals, by improving animals' capacity to use human signals to adapt their behaviour, by decreasing fearfulness toward humans and increasing attention toward humans (Mignon-Grasteau et al. 2005). Domestic species form particular relationship with humans. In farms, this relationship is important for animal welfare. Therefore understanding the mechanisms of emergence and maintenance of a positive human-animal relationship (HAR), by studying human-animal interactions and their consequences would have applications for welfare (Rault et al. 2020). Animal welfare conveys three major aspects: the ability of an animal to control its mental and physiological stability (Broom 2011), the decrease of negatively perceived as well as the increase of positively perceived contexts and species-specific behaviors (Peterson, Simonsen, and Lawson 1995; Weerd and Day 2009). A positive HAR is thought to be established through repeated positive interactions between the human and the non human animal, accumulating positive experiences though positive associative learning, modifying cognitive biaises, generating expectations from the non human-animal toward the human and can be appreciated through behavioural and physiological measures as well as the expression of positive emotions (reviewed in (Rault et al. 2020)). Several behavioural measures may help to define a positive HAR such as: short latency to approach and spatial proximity (Schmied et al. 2008; Boivin, Tournadre, and Le Neindre 2000), body postures (Villain et al. 2020b) or play behaviour (Jerolmack 2009). Contacts from a human such as stroking, may induce changes in body postures and exposition of body areas by the animal to the human, suposedly vulnerable [central neck area in cattle (Schmied et al. 2008), abdominal area in pigs (Rault

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et al. 2019) . Such grooming solicitation may be markers of engagement, trust and motivation to interact with the human. In most cases, these behaviors are similar to those shown during intraspecific sociopositive interactions, although there are some interspecies specific behaviors (e.g., dog vs. wolf (Gácsi et al. 2005)). Vocal behaviour may also help defining the quality of a HAR. First, vocalisations are known to carry markers of the emotional states in several bird and mammal species (Briefer 2012; 2020) and this has been extensively study in domestic farm animals reviewed in (Laurijs et al. 2021). Second, some vocalisations have been associated to positive interactions with or care soliciting from humans, for example the cat – human communication : purring is thought to be derived from mother pup communication during nursing and is oberved associated to care sollicitation from humans ; meowing, which is not observed during intra specific interactions is thought to emerge from associative learning during cat – human interactions (Brown and Bradshaw 2014). This shows that HAR may elicit specific vocalisations from the non human animal toward the human.

In pigs, numerous evidence attest the possibility of a positive HAR. Animals may be tamed by humans providing regular additional positive contacts, leading to the expression of positive perception of humans, with evidence from behavioural and physiological studies. Cognitive bias tests showed a positive judgment bias in piglets that had received gentle contacts with humans (Brajon et al. 2015a). Pigs may recognise a carying human compared to unfamiliar and adapt their behaviour accordingly (Brajon et al. 2015c). Pigs may be sensitive to human voice and respond accordingly (Bensoussan et al. 2019; 2020). Pigs vocalisations are diverse and linked to their emotional states, attested by the use of positive or negative vocal signals (Briefer et al. 2019; 2022; Tallet et al. 2013) . Indeed, even within a call type, spectro temporal changes are closely linked to the valence of a situation or the intensity of a perceived situation. For example, grunts, that are one of the most used vocal signals and in various situations is now known to be a flexible call: shorter grunts have being associated to positive situations (Briefer et al. 2019; 2022; Friel et al. 2019; Villain et al. 2020a), as well as higher formant and a lower fundamental frequency during positive situations (Briefer et al. 2019; 2022; Villain et al. 2020a; Friel et al. 2019) . Grunt structure may also change according to the arousal of a situation, with a higher frequency range and a higher bandwidth when produced in a more intense positive situation (Linhart et al. 2015). In order to determine if vocalisations may be used as non invasive indicators of the quality of human-pig relationship by themselves, we tested whether they could encode the quality of the human-piglet relationship. We predicted that if grunts carry information on the quality of the human-piglets relationship, then 1. A period of positive interactions given by a human should modulate vocal quality of piglets when in presence of the

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human, leading to grunts exhibiting markers of positive states (shorter grunts), 2. spatial proximity toward a human being should influence the vocal activity (higher pitched grunts as the arousal increases).

Methods

Ethical note

The study was approved by the ethic committee CREEA and received the authorization no. APAFIS#17071-2018101016045373_V3 from the French Ministry of Higher Education, Research and Innovation; and was in agreement with the French and European legislation regarding experiments on animals.

Subjects and housing conditions

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

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

Experimental treatment : human additional contacts – taming period

From day 28 to day 39 of life, piglets were separated into two treatment groups as follows:

- Untamed piglets, a group with minimal human contact, H group: Control piglets from 10 rearing pens received the minimal amount of daily contact with a stockperson (a 1.70m tall male who did the feeding, cleaning and health checkups). The stockperson wore a dark green shirt and pants and brown shoes.
- Tamed piglets, a group receiving additional human contacts, H+ group: in addition to the daily care given by the same stockperson as for H group, piglets from the 10 other rearing pens received sessions of additional human contacts with one of the two experimenters (both women, both between 1.70-1.73 m tall, balanced number of pens attributed to each of them). The experimenters wore the same blue overalls and green boots each time they interacted

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with the piglets. There were twenty-nine sessions of 10 minutes of interactions, from day 28 (weaning) until day 39, occurring five days a week. Three sessions per day were performed (except on the day of weaning during which only two were done with a two-hour break in between). Each session took place in the rearing pen and the order of the interventions in the pens was balanced across days. The handling procedure, using gentle tactile contacts is described in supplementary material of Villain et al. (2020a) and was similar to Tallet et al. (2014).

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

Piglets were habituated to the test room for 10 minutes, by pen, two days before the start of the conditioning. The conditioning took place between day 42 and 62 after weaning and lasted twelve days, with two trials per day and at least three hours between trials on the same day. The experimental design of the conditioning is already published (Avelyne S. Villain et al. 2020a). Briefly, all piglets were individually trained to learn to associate two different stimuli with the arrival of two different (pseudo)-social partners: either two pen mates (partner = Conspecifics) or a familiar human (partner = Human). When entering the room, the piglets and the partner(s) would remain in the room for two minutes. Specifically, when the human entered, they sat on a bucket and positively interacted with the piglet, in the same manner as additional contacts was provided to the tamed piglets during the taming period (see above section) (figure 1). Hens, at the beginning of the conditioning phase, tamed piglets were already familiar with the human from the taming period, whereas untamed were unfamiliar with the human and only became familiar during the sessions of additional positive contacts of the conditioning. Since additional positive contacts occurred during the conditioning for both treatment groups (H and H+) the human could be considered as familiar for all piglets at the end of the conditioning, with a different degree of familiarity between the two groups. For every second trial, the two-minute reunions with the human were analysed : trials number 2, 4, 6, 8, 10 and 11.

Standard Isolation/Reunion Tests

At 40 or 41 (before conditioning) and then 63 or 64 (after conditioning) and days of age, pigs were subjected to a standard Isolation/Reunion test in order to assess their perception of the human . The test consisted of two phases. The pig was brought individually in a trolley to the experimental room. It was left alone for five min, which defined the ‘Isolation’ phase. Then, the human entered the room, remained stand up for 30 secondes before they sat on a bucket, remaining silent and not moving for 4.5 minutes (figure 1).

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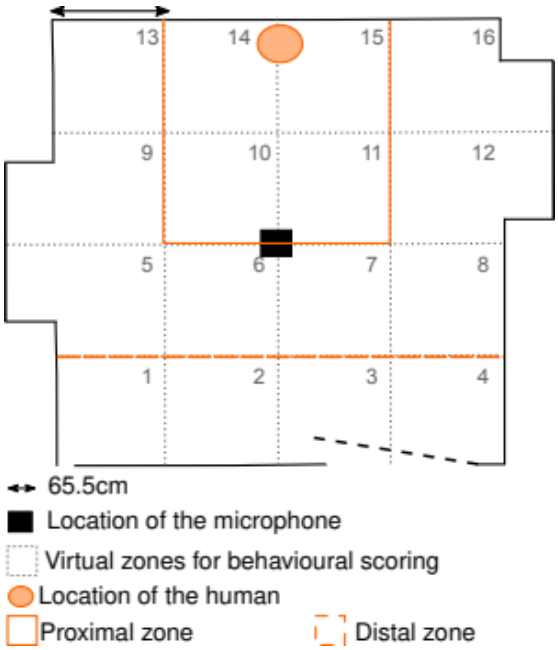

Figure 1: Design of the room used during the isolation/Reunion tests and the additional positive contact sessions of teh conditioning. ther room was split into 16 virtual zones and proximal and distal zones to the human regarding the position of the tested piglet.

Behavioural monitoring and analyses

Behaviours were monitored using a camera (Bosh, Box 960H-CDD) and annotated using *The Observer XT 14.0* (Noldus, The Netherlands) software. The square room was split into 16 virtual equally-dimensioned zones to assess the mobility and exploratory behaviour of the piglet. A proximal zone, around the human was defined by merging four zones, a distal zone was defined merging the four most distant zones from the human (figure 1).

The behaviours scored during the reunion of the Isolation/Reunion test and the sessions of additional positive contacts of the conditioning are available in table 1. Every time the shoulders of the piglet crossed a zone, a zone change was scored. Looks and watching behaviours were quantified as when the piglet turned its head toward the human or looked up at the room, and scored as point events, all over behaviours were scored as state events. Behavioural scores were then calculated to quantify global responses (see below).

Table 1: Ethogram.

Behaviour	**Description**
Nb zones crossed [1,2]	The number of times the piglet crossed a virtual zone

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Nb approaches H [1]	Number of times the piglets entered the proximal zone
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
Nb looks toward H [1,2]	The number of times the piglet looked at the human
Nb looks other than H [1]	The number of times the piglet looked at other parts of the room
Time watching room [1]	The number of times the piglet watched other parts of the room than the human
Time in proximal zone [1,2]	The amount of time the piglet spent in the proximal zone
Time in distal zone [1,2]	The amount of time the piglet spent in the distal zone
Time in contact H [1,2]	The amount of time the piglet investigated the human
Time investigating room [1,2]	The amount of time the piglet investigated the room
Nb contacts H [2]	Number of times the piglet was in contact with the human (initiated by the piglet or the human)

[1]: Scored for Reunion of Isolation/Reunion tests. [2]: Scored for reunion of conditioning sessions

Acoustic monitoring and analyses

Vocalisations were recorded with an AKG C314 microphone placed in the center of the room and one meter above the ground, connected to a Marantz MD661MK2 recorder. Vocalisations produced during each phase of the trial were manually annotated according to vocal type (grunt, squeak, bark, scream and mixed calls), after visual inspection of spectrograms on Praat software. Only grunts were analysed further as they were the most frequently expressed. A spectro-temporal analysis was performed with custom-written codes using the Seewave R package (Sueur, Aubin, and Simonis 2008) implemented in R (R Core Team 2015) . We first studied the spectral properties of the remaining background noise of the experimental room (electric noises and remaining low frequency noises from the rest of the building), using 20 examples of 0.5 second fragments. Since the first quartile (Q25) of the normalized spectrum of the background noise was 250Hz and the grunts are low frequency vocalisations, we decided to remove all frequencies below 200Hz in order to focus on the most relevant frequencies, using a 0.2-8 kHz bandpass filtering ('fir' function). As a consequence, all results presented in this study are on a 0.2-8kHz frequency range, and no conclusions on possible frequency components of grunts below this 200Hz threshold can be drawn here. A standardised grunt was detected when the amplitude crossed a 5% amplitude threshold

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('timer' function) to measure the duration. After amplitude normalisation, the following spectral parameters were calculated using the 'specprop' function (FFT with Hamming window, window length = 512, overlap = 50%): mean, first (Q25) and third (Q75) quartiles, interquartile range (IQR), centroid and standard deviation (all in Hz). The grunt dominant frequency (in Hz) was also calculated ('dfreq', 50% overlapping FFTs, window length = 512), which is the mean over the grunt duration of the frequencies with the highest level of energy. Frequency peaks were detected and the minimal and maximal peaks were kept as descriptors ('fpeaks' function, window length = 512, peak detection threshold = 10% of the normalized amplitude) Parameters measuring noisiness and entropy of the grunts were: Shannon entropy (sh), Spectral Flatness (Wiener entropy, sfm) and Entropy (H) [combining both Shannon and Temporal envelop entropy, length = 512, Hilbert envelop). Two linear acoustic parameters were used: the logarithm of grunt duration and a built-in spectral acoustic score with all spectral parameters (see below). Table of acoustic data available in supplementary material (table S4).

Statistical analyses

Behavioural and vocal response scores

In order to take into account correlated parameters and reduce the number of variables tested as response variables in statistical models, all parameters having a symetrical distributions were used in principal component analyses ('pca' function from 'ade4' R package (Dray and Dufour 2007, 4)). All PCs having an Eigen value above one were kept and constituted response scores for behavioural ('ReuPCs' and 'CondPCs' table 2 and 3 respectively) and vocal parameters ('AcPCs', table 4). Only the duration of grunts was kept separated from the spectral parameters to keep it as a temporal parameter.

Table 2: Behavioural response score for the reunion phase of the Isolation/Reunion test. Percentage of explained variance and variable loadings of the principal component analysis. The first three PCs constituted three behavioual scores. Parameters that explain the most each PC are bolded (|loading|>0.4).

	ReuPC1	**ReuPC2**	**ReuPC3**
Cumulative variance explained %	38.3	60.8	74
Nb zones crossed	24.177	**-55.843**	-0.435
Nb approaches H	**47.748**	-30.163	0.578
Time watching H	**-52.914**	-7.422	25.585
Latency to contact H	**-64.232**	-0.464	1.688
Nb looks toward H	-7.787	**-43.721**	31.633

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Time watching room	-32.048	-13.581	-6.238
Nb looks other than H	3.524	**-72.408**	-2.027
Time in proximal zone	**69.96**	-0.156	9.584
Time in distal zone	**-46.416**	-12.437	-1.215
Time in contact H	**61.041**	3.586	24.183
Time spent investigating room	11.868	-7.503	**-42.265**

Table 3: Behavioural response score for the reunions of additional positive contacts during the conditioning. Percentage of explained variance and variable loadings of the principal component analysis. The first three PCs constituted three behavioual scores. Parameters that explain the most each PC are bolded (|loading|>0.4).

	CondPC1	**CondPC2**	**CondPC3**
Cumulative variance explained %	41	68.5	80.7
Time in proximal zone	**80.23**	2.542	-0.112
Time in distal zone	-33.826	8.547	30.789
Number of contacts H	**78.55**	6.476	2.288
Time in contact H	**86.625**	0.715	-0.369
Nb looks toward H	-2	**79.898**	-0.745
Time watching H	-6.757	**65.67**	-10.325
Nb zones crossed	0.129	33.599	**48.457**
Time spent investigating room	0.006	**-49.286**	14.205
Latency to contact H	**-81.01**	-0.248	-2.83

Table 4: Variable loadings of the first three principal components (i.e having an Eigen value above one)following a principal component analysis (pca function, ade4 R package) on all the grunts recorded in the entire dataset (including both types of tests, N=17 546 grunts). The transformations used to reach symetrical distribution before the PCA are indicated in parenthesis. Parameters that explain the most each PC are bolded (|loading|>0.4) .

	AcPC1	**AcPC2**	**AcPC3**
Cumulative variance explained %	59.769	76.807	87.712
Mean Dominant Frequency[1]	-13.558	**53.557**	2.220
Min frequency peak[1] (log)	-0.349	**58.758**	24.236
Max frequency peak[1]	**-43.023**	8.760	-9.537
Mode[2] (log)	-0.522	**66.248**	19.268

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Mean[2] (log)	**-95.092**	-2.295	2.028
Q50[2] (log)	**-85.278**	0.280	-0.093
Q25[2] (log)	**-52.360**	19.327	0.985
Q75[2] (sqrt)	**-88.925**	-4.645	2.309
Centroid[2] (log)	**-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

Statistical models

All statistics were carried out on R (R Core Team 2015). Linear mixed effect models were built ('lmer' function, 'lme4' R package (Bates et al. 2014)) when studied parameters were linear (behavioural and vocal PC scores grunt duration) and one binomial generalized mixed effect model was built for binary parameters (occurrence of missed contacts initiated by human during the conditioning). In all models described below, the identity of the replicate ('1' or '2') was used as interacting fixed factor, since the experiment was run in two identical replicates on two independent groups. The identity of the human ('AH' or 'AV') was used as interacing fixed factor in all models described below, since two experimenters were involved in taming the piglets (but always the same human was attributed to a piglet). The piglet was used as random factor to take into account the within subject design in all models. The following subsections describe how models were built for each type of tests.

Isolation/Reunion tests

The aim of this part was to test the effect of the taming treatment (H vs. H+ piglets) and additional human contacts during sessions of the conditioning on piglet's reaction to human presence. Since the

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same Isolation/Reunion test was repeated before and after the conditioning, we used the parameter 'Conditioning time' as a two level interacting factor ('before' or 'after' the conditioning) to test the effect of the conditioning. Only the behaviour of the piglet during the 4.5min reunion with the sitted human was analysed.

```
Model 1 <– lmer ( Response variable ~ Treatment*Time + Treatment*Replicate +
Treatment *Human + Time*Replicate + Time*Human + (1 | piglet ID), data=
dataBehaviourReunion).
```

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

```
Model 2 <– lmer ( Vocal    variable ~ Treatment * Phase * Time + Treatment *
Human + Time * Human + Treatment * Replicate + Time * Replicate  + (1 | piglet
ID/time/Phase) , data= dataVocalIso + dataVocalReunion).
```

To go further, only the reunion phase was kept and a proximity parameter was added. Indeed, the piglet could vocalise either when near the human or away from her and this spatial proximity was demonstrated as an important factor of changes of vocal features (Villain et al. 2020b). Thus, a two level proximity factor was built : either '1' when the piglet was in the proximal zone (figure 1) or '0' when it was elsewhere in the room.

```
Model 3 <- lmer ( Vocal response parameter ~ Treatment * Time* In Prox. Zone +
Treatment * Human + In Prox. Zone * Human + Treatment * Replicate + In Prox.
Zone * Replicate + Time * Replicate + Time * Human + (1 | piglet ID/Time), data
= dataVocalReunion).
```

Conditioning trials

The aim was to study the evolution of human-piglet relationship along the conditioning [the variable 'Trial number', used as a continuous variable], depending on the previous experience piglets had with the human [either already familiar (H+ group) or unfamiliar (H group) at the beginning of the conditioning]. Trial number was also used as a random slope to take into account individual trajectories (Schielzeth and Forstmeier 2009). The following model was built to test the behavioural response scores (lmer) and the occurrence of missed contact initiated by the human during a session (presence/absence, binomial model, glmer):

```
Model 4  <– (g)lmer ( Behavioural Response variable ~ Trial * Treatment + Trial
* Human + Trial * Replicate + Treatment * Replicate + Treatment * Human + (1+
Trial | piglet ID), (family=Binomial), data= dataBehaviourConditioning).
```

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

```
Model 5 <- lmer (Vocal Response variable ~ Trial number * Treatment *
InProximalZone+ Trial number * Human + Trial number * Replicate + Treatment *
Replicate + Treatment * Human + Human * InProximalZone + Replicate *
InProximalZone + (1+ Trial | piglet ID), data= dataVocalConditioning).
```

Model validation and statistical tests

All linear models were validated by visual inspection of the symmetrical and normal distribution of the residuals. Anovas ('car' R package (Fox and Weisberg 2011)) were computed on models to test for significant effects of explanatory variables. Following the Anova, when interactions were found significant, post hoc test were run on model interactions, correcting for multiple testing with Tukey contrasts ('emmeans' or 'lstrends' functions from 'emmeans' R package (Lenth 2016), for categorical or continuous variables repectively). Results of the Anova, model estimates and pairwise post hoc comparaisons computed are reported in the supplementary material (tables S1 and S2 for tests, table S3 for model estimates).

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Results

Effet of the conditioning process on piglets' reaction to human presence (Isolation/Reunion tests)

Untamed piglets express a similar behavioural proximity to a human after a positive conditioning than tamed piglets

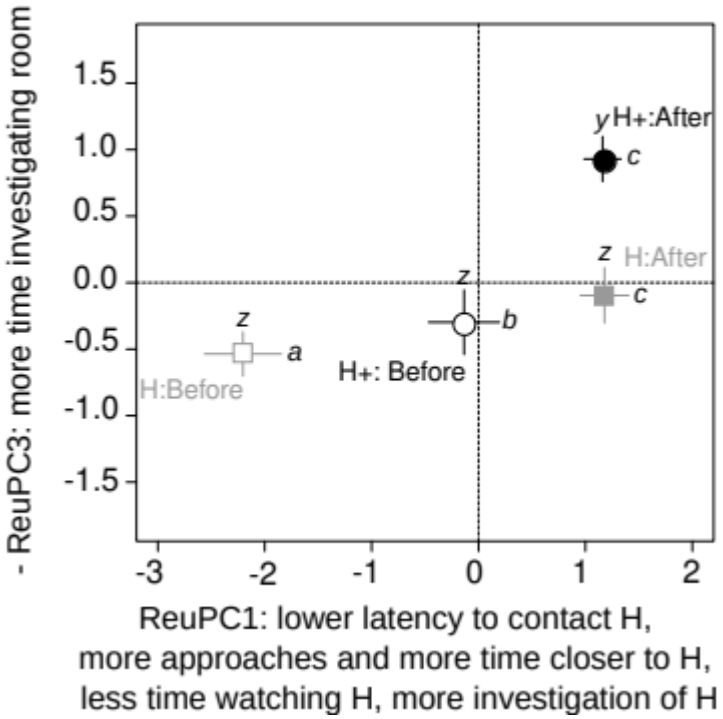

Figure 2: Effect of conditioning and treatment on spatial behaviour and proximity toward the human during a post isolation reunion test. Mean +- SE per group is indicted, different letters indicated significantly different groups. Significant interaction between treatment (H : grey squares and H+ : black circles) and time (Before the conditioning: empty elements and After the conditioning: filled elements) on behavioural PC1 (letters a to c) and PC3 (letters z and y). Full statistical report is available as supplementary material (tables S1 S2 for statistical tests and S3 for model estimates)

The interaction between the treatment (piglets tamed before the conditioning (H+) or not (H)) and the conditioning time (before or after the conditioning) was significant for both ReuPC1 and ReuPC3 ($\chi^2_1 = 28.0$, $p < 0.001$, and $\chi^2_1 = 3.7$, $p = 0.05$ respectively, figure 2) but not for ReuPC2 ($\chi^2_1 < 0.001$, $p = 0.99$, supplementary table S1). Post hoc tests on ReuPC1 showed that ReuPC1 was higher after the conditioning than before (H: after – before, t.ratio = 12.1, $p < 0.001$, H+: after – before t.ratio =

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11.0, $p < 0.001$) and that before the conditioning, tamed piglets had significantly higher ReuPC1 than untamed piglets (Before, H – H+: t.ratio = -2.1, $p < 0.001$), but not after (After, H – H+: t.ratio = 0.02, $p = 1.0$). According to the loadings, this means that tamed piglets had lower latency to contact the human, approached her more often and spent more time close to and investigating the human (ReuPC1) than untamed piglets before the conditioning. This score increased after the conditioning and no evidence of a difference between treatments after the conditioning was found (figure 2). Post hoc tests on ReuPC3 showed an significant effect of the conditioning time only in tamed piglets (H+: after – before, t.ratio = 5.2, $p < 0.001$, H: after – before, t.ratio = 2.6, $p = 0.06$). No difference in ReuPC3 was found between treatments before the conditioning (Before: H – H+, t.ratio = -0.75, $p = 0.87$), whereas tamed piglets had a higher -ReuPC3 after the conditioning than before (After : H – H+, t.ratio = -3.2, $p = 0.009$). According to the loadings, this means that tamed piglets expressed more investivation of the room after the conditioning than before. No evidence of any effect on ReuPC2 was found (table S2).

Taming decreases grunt duration even when no human is present with the piglet

Comparing the effect of the phase of the test (Isolation vs. Reunion with the human), taking into account the conditioning time and the treatment, no evidence of any effect of neither the three way interaction ($\chi^2_1 < 0.62$, $p > 0.43$) nor two way interactions of interest were found (treatment: phase, conditioning time:phase, conditioning time: treatment interactions : $\chi^2_1 < 3.5$, $p > 0.06$, table S2) in any of the scores. However, grunts produced by tamed piglets were shorter than grunts produced by untamed piglets ($\chi^2_1 = 5.5$, $p = 0.02$, estimates of log(duration)[95% confidence interval]: -1.25[-1.32;-1.19] and -1.12[-1.2;-1.1] respectively in tamed and untamed piglets, table S3). Single effects of the phase of the test were significant for grunt duration and all AcPCs ($\chi^2_1 > 6.6$, $p < 0.01$, table S1). Grunts produced during the reunion phase with the human were shorter (estimates of log(duration) : -1.32[-1.37;-1.26] vs. -1.06[-1.12;-1.00]) and, according to the loadings, grunts produced during the reunion phase had a higher frequency range, higher bandwith and noise component (-AcPC1: 0.78[0.48;1.08] vs. 0.34[0.03;0.66]), higher pitched (AcPC2: -0.18[-0.36;0.01] vs. -0.46[-0.65;-0.28]) and their spectrum had a higher skewness and kurtosis (AcPC3: -0.25[-0.37;-0.14] vs. -0.11[-0.23;0.01]), compared to the isolation phase.

The conditioning process attenuates the effect of proximity on grunts vocal features in untamed piglets

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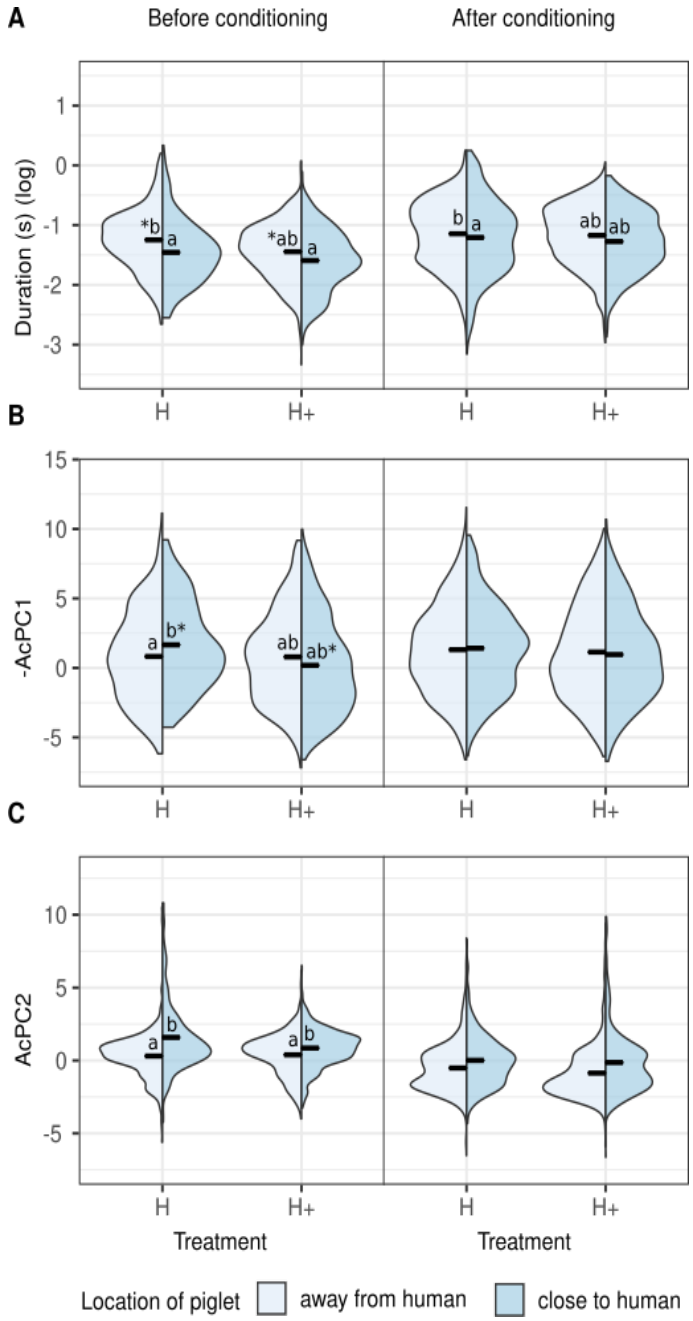

Figure 4: Acoustic structure of grunt during the reunions with a silent and static human (isolation/reunion test): effect of conditioning (before or after), treatment (H: light grey, H+: dark grey), and location of the piglet relatively to the human (close: dark blue or away from them: light blue). Violin plots representing the median and the density of data distribution in the considered group. Results from the three way interaction between the treatment, the conditioning time and the location, on a subset of data considering only the reunion part of the test , the conditioning time was fixed to allow pairwise comparison of interacting location and treatment on grunt duration (A) and the first acoustic score (-AcPC1, B) and the second acoustic score (AcPC2, C). Letters represented significantly different groups ($p < 0.05$) and 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).

337

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During the five-minute reunion, the piglet was scored either as close to the human or away from them. The three way interaction of the conditioning time, the treatment and the location was significant for grunt duration, -AcPC1 and AcPC3 ($\chi^2_1 > 4.9$, $p < 0.03$). Post hoc tests revealed that grunts produced closer to the human were shorter than the ones produced further away, but only in untamed piglets, effect being stronger before the conditioning than after it (H piglets : away – close, z.ratio = 6.3, $p < 0.001$ before and z.ratio = 4.1 $p < 0.001$ after the conditioning, H+ piglets : away – close z.ratio < 1.98 $p > 0.19$, figure 3A). -AcPC1 was higher, i.e grunts had a higher frequency range, bandwith and were noisiness when produced closer to the human than further away, but only in untamed piglets and before the conditioning but not after (H piglets : away – close, z.ratio = -3.34, $p = 0.005$ before and z.ratio = -1.23 $p = 0.61$ after the conditioning, H+ piglets : away – close z.ratio < 0.36 $p > 0.21$, figure 3B). For AcPC2, the three way interaction was close to reach significant level ($\chi^2_1 = 3.3$, $p = 0.07$), thus, for conservative purposes, the results of the posthoc tests of the three way interaction are presented (see two way subsequent interactions comparisons in supplementary tables S2 and S3). Before the conditioning, AcPC2 was higher when piglets were closer to the human and this effect was stronger for untamed piglets than tamed ones (away – close, H : z.ratio = -5.54 $p < 0.001$, H+ : z.ratio = -3.56 $p = 0.002$, figure 3C), meaning the grunts were higher pitched when produced closer to the human. This effect did not remain true after the conditioning as no evidence of any difference between treatments and location was found (|z.ratio| < 2.4 $p > 0.09$,). For AcPC3, post hoc tests did not reach significant levels (|z.ratio| < 2.3 $p > 0.09$ for any comparison) .

Emergence of positive perception of human (effect of additional positive contacts sessions along the conditioning)

The conditioning process increases behavioural proximity

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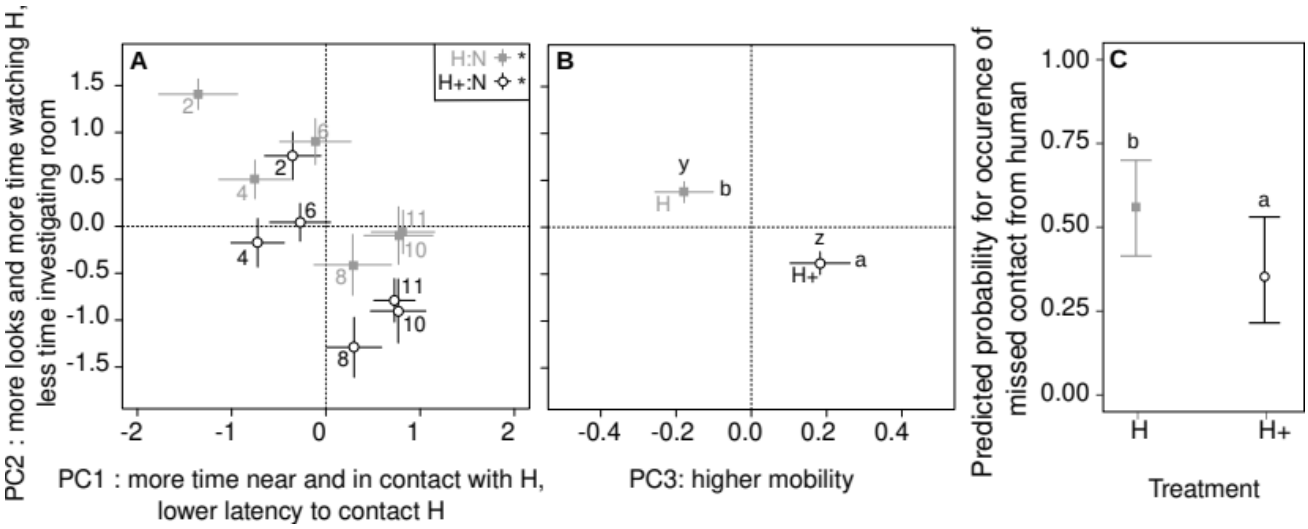

Figure 5: Effect of trial number over the conditioning on spatial behaviour and proximity to human during the 2min sessions of additional positive contacts during reunions of the conditioning. A and B: Mean +- SE per group. A: Single effect of trial number on behavioural PC1 and PC2 according to treatment (H: grey, H+: black). B: Single effect of treatment on behavioural PC3 and PC2.C and D : predicted probability of occurrence of at least one failed contact from the human, mean estimates +- 95% confidence interval from the generalized mixed effect model. C: single effect of treatment,. Stars in the legend box represent significant effect of the trial number (A), different letters represent significantly different groups (B and C). Full statistical report is available as supplementary material (tables S1 et S2 for statistical tests, table S3 for model estimates).

No evidence of any effect of the interaction between the treatment (tamed piglets before the conditioning H+ or not H) and the trial number was found for all behavioural scores (CondPC1, CondPC2 and CondPC3, table 3). Independently from the treatment, the higher the trial number was the higher CondPC1 was (χ^2_1 = 59.3, p < 0.001, slope estimate [95% confidence interval]: 0.20 [0.15 : 0.25]) and the lower CondPC2 was (χ^2_1 = 48.6, p < 0.001, slope estimate: -0.17 [-0.22 : -0.12]). According to the loadings, over the conditioning, piglets decreased the latency to contact the human, made more contacts, spent more time in the proximal zone and in contact with the human (condPC1), decreased the number of looks to the human, spent less watching the human and more time investigating the room (CondPC2) (figure 4A). Independently from the trial number, tamed piglets had a lower CondPC2 and a higher CondPC3 than the ones from the H group (χ^2_1 = 12.8, p < 0.001 and χ^2_1 = 7.0, p = 0.008 respectively), meaning that tamed piglets expressed a fewer number of looks to the human, spent less time watching them and more time investigating the room (CondPC2) and crossed more virtual zone during the test (CondPC3) (figure 4B). The probability of having at least one missed contact by the human during a session was lower for tamed piglets than untamed ones (χ^2_1 = 9.57, p = 0.002, figure 4C), with no interaction with the trial number (χ^2_1 = 0.22, p = 0.064).

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Grunt acoustic features depends on spatial proximity to human

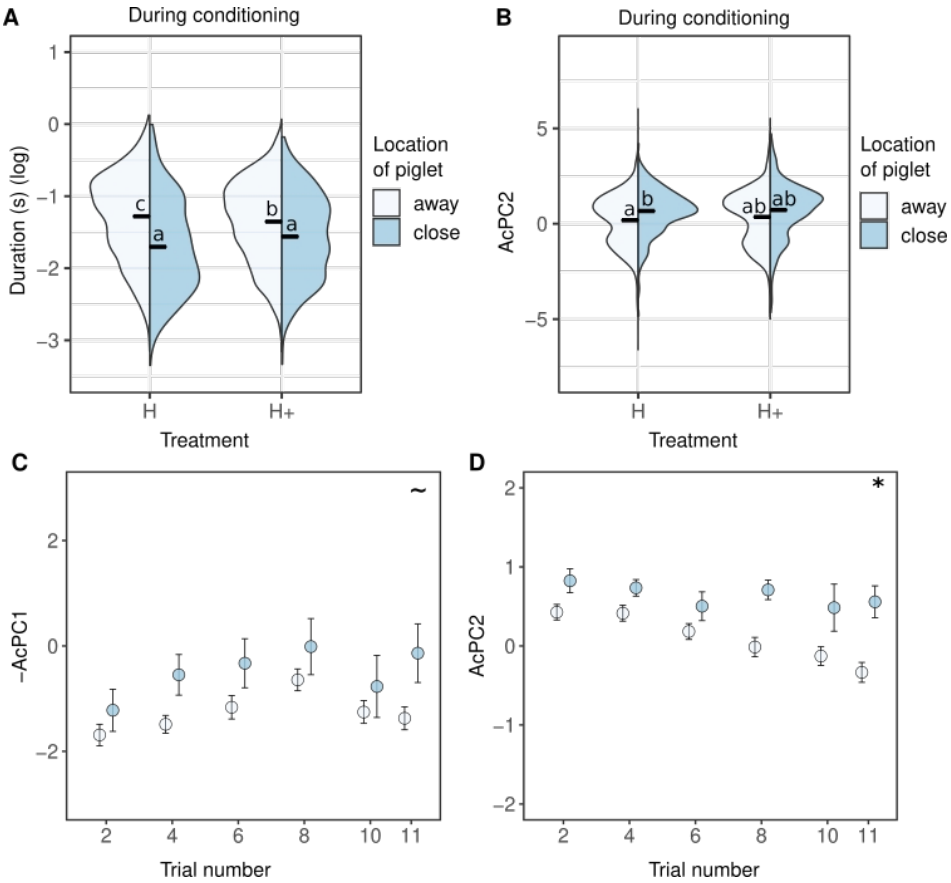

Figure 6: Evolution of acoustic paramters over the conditioning, depending treatment and location of piglets, during the 2min sessions of additional positive contact reunions.. A-B : Violin plots representing the median and the density of data distribution in the group. C-D : Mean +- SE per group, BA-B: Interacting effect of the treatment and the location of piglets (in proximal zone of the human: dark blue or away from the human: light blue) on grunt duration (A) and AcPC2. C-D: Interacting effect of trial number and location of piglet on -AcPC1 (C) and AcPC2 (D). Different letters in A and B represent significantly different groups, "" in D represents significant difference between slopes and "~" in C a trend. . Full statistical report is available as supplementary material (tables S1-S3).*

During the sessions of additional positive contacts of the conditioning, the three-way interaction between the trial number, the treatment and the location was not significant for any of the acoustic scores ($\chi^2_1 < 0.18$ $p > 0.67$), allowing the analysis of the two way interactions of interest. The interaction between treatment and the trial number was not significant for all acoustic scores ($\chi^2_1 < 2.5$ $p > 0.11$), however grunt duration decreased over the conditioning sessions (trial number:replicate interaction, $\chi^2_1 <= 5.3$ $p = 0.02$, slope estimate -0.03[-0.04;-0.01] for the lower slope, table S1 and S3). Independently from the trial number, grunt duration was lower when piglets were located close to the human and this effect was stronger in untamed piglets than tamed piglets

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(treatment:location interaction: χ^2_1 = 15.8 p < 0.001, away vs. close, H piglets: z.ratio = 10.2 p < 0.001, H+ piglets: z.ratio = 6.86 p < 0.001, figure 5A). AcPC2 was higher when piglets were close to the human, but only in untamed piglets (treatment:location interaction, χ^2_1 = 7.6 p = 0.005, pairwise comparisons away vs close, in H: z.ratio = -4.9 p z 0.001 and in H+: z.ratio = -2.0 p = 0.21), meaning that untamed piglets produced higher pitched grunts when closer to the human (figure 5B). The effect of the location on -AcPC1 and AcPC2 depended on the trial number (trial number : location interaction, χ^2_1 = 3.97 p = 0.05 and χ^2_1 = 6.1 p = 0.01 respectively): -AcPC1 and AcPC2 were higher when closer to the human with a greater extent later in the conditioning than earlier (slope comparison away – close, -AcPC1 : z.ratio = -1.80 p = 0.07, AcPC2 : z.ratio = -2.34 p = 0.02). . According to the loadings, this means that the frequency range, bandwith and noisiness of grunts (-AcPC1) as well as the pitch (AcPC2) decreased over the conditioning when piglets were located away from the human but remained high when piglets were close (figure 5C and 5D).

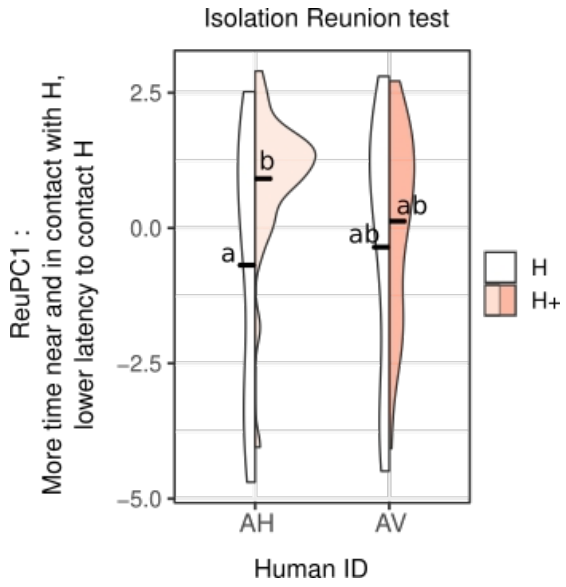

Figure 7: Effect of human identity on spatial behaviour and proximity during standard isolation reunion tests. Violin plots representing the median and the density of data distribution in the group. Different letters represent significantly different groups. Full statistical report is available as supplementary material (tables S1 and S2 for statistical tests, table S3 for model estimates).

Since half of the piglets had been assigned to one human experimenter and the other half to another one, this allowed the analysis of the effect of the identity of the human on behavioural and vocal scores. During the reunions of the Isolation/Reunion test, the behavioural proximity score (ReuPC1) was higher when piglets were tamed by the human 'AH' (treatment: human ID interaction, χ^2_1 =

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6.01, p = 0.01, pairwsie comparison H vs H+, AH: t.ratio = -4.77, p < 0.001, figure 6). When the human 'AV' tamed the piglets, ReuPC1 scores exhibited intermediate values and not significantly different score between treatments (AV, H vs H+: t.ratio = -1.33, p = 0.56). This effect of the human identity on behaviour was not found considering the reunions of the conditioning (χ^2_1 < 1.32, p > 0.25 for all CondPCs, table S1).

Table 5: Significant effects of human identity on vocal parameters (AcCP1 and AcPC2) during the reunion of the Isolation/Reunion test and during the sessions of addiitonal 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').

Acoustic parameter	Fixed effect	Levels	Estimate	Lower.95%CI	Upper.95%CI	Statistic	P-value
Reunion of the Isolation/Reunion test							
AcPC2	Human ID	AH	0.154	-0.119	0.427	χ^2_1= 4.94	P = 0.03
		AV	-0.292	-0.571	-0.012		
Sessions of additional positive contacts of the conditioning							
-AcPC1	Human ID	AH	0.091	0.037	0.144	χ^2_1 = 4.69	P = 0.03
		AV	0.076	0.021	0.132		
AcPC2	Human ID*In prox. zone	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		
AcPC3	Human ID * 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		

Considering the acoustic scores, no effect of human identity was found on AcPC1 during the Isolation/Reunion tests but -AcpC1 was higher when the human 'AH' was in the room during the

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reunion periods of the conditioning (table 5), meaning the frequency range and the bandwidth of the grunt were higher when the human 'AH' interacted with the piglet compared to the human 'AV'. AcPC2 was higher when the human 'AH' was in the room during the Isolation/Reunion tests (table 5), meaning that the pitch of grunts was higher and this effect was also found during the sessions of additional positive contacts of the conditioning in interaction with the location of the piglet (χ^2_1 = 11.9, p = 0.001): although, AcPC2 increased when piglets were located close to the human, this increase was significant only for the human 'AV'and not for 'AH' (table 5). AcPC3 was not different between humans during the reunions of the Isolation/Reunion tests but, over the conditioning, AcPC3 changed differently when piglets were tamed by the human 'AH' or 'AV', as showed by the significant interaction between trial number and human identity (χ^2_1 = 8.0, p = 0.005): the skewness and kurtosis of grunts decreased over the conditioning when 'AH' was interacting with the piglets, but not 'AV' (see slope estimates, table 5). No evidence of any effect of human identity was found on grunt duration neither during the Isolation/Reunion tests nor during the sessions of additional positive contacts of the conditioning (table S1).

Discussion

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

The standard reunion test with the human before the conditioning showed that the taming treatment succeeded in creating two different levels of human-piglet relationship (H and H+), as tamed piglets expressed a higher attractiveness toward the human (ReuPC1) than untmaed piglets, parameters considered as indicators of a positive HAR (Rault et al. 2020). This test also showed that the conditioning modified the behaviour of untamed piglets so that they finally expressed a similar attractiveness toward the human as tamed piglets, after the conditioning. So it seems that the conditioning process allowed untamed piglets to compensate the lack of taming before the conditioning and develop a positive perception of the human. In addition, tamed piglets expressed more exploratory behaviours than untamed piglets after the conditioning (ReuPC3), which may be interpreted as natural foraging and disinterest from human contact, which may be a sign of positive welfare (Weerd and Day 2009). However, this could be interpreted also in terms of attachment to the human. Indeed, attachment to a human may facilitates exploration of novel environments or objects, as shown in dogs (Palmer and Custance 2008). Attachment has already been hypothesised in the lambs-human relationship (Tallet, Veissier, and Boivin 2009).

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The analysis of piglets' behavior every second sessions of the conditioning showed that, over time and for both treatments (H and H+), piglets expressed less fear (CondPC2), a higher attraction toward the human (CondPC1) and avoided less the human when the later attempted to interact with them. As a conclusion, two- minute daily sessions of additional positive contacts did change positively the perception of the human for the piglets, and thus their willingness to interact with them. Since no evidence of any interaction between time and treatment was found, no conclusion of differential developmental trajectories between treatments can be drawn, but a parallel development of the human-piglet relationship in both groups, when considering the conditioning sessions (and not the standard reunion tests). Over the conditioning sessions and similarly to the observations during the standard reunion test, tamed piglets expressed higher mobility and room investigation behaviours. This may allow us to generalize our hypothesis on attachment described above : taming may provide an environment secure enough for the piglets to explore their environrment in the presence of the human. Overall, the behavioural monitoring showed that two minute sessions of positive additional contacts per day are sufficient to increase proximity to a human to similar levels as when piglets were previously familiarised for 2 weeks, even when piglets experienced social isolation, but it did not allow the piglets to express natural exploratory behaviours as the previously tamed piglets.

Links between vocal expression and positive HAR

In this study, piglets were subjected to two type of interactions with the human : during the standard reunion test, no movements nor speech was produced by the human, during the sessions of additional positive contacts of the conditioning, the human provided contact and produced speech toward the piglet. These types of interactions had different effects on vocal expression, which allow us to evaluate the origin and functions of the vocal flexibility expressed in grunt stucture, first studying the standard reunion test first and the sessions of additional positive contacts after.

Human mere presence affects vocal expression according to previous experience

Social isolation was associated to longer and lower pitched grunts with a down shifted frequency spectrum. A reunion with a static human changed grunt structure to shorter, higher pitched with an up shifted frequency spectrum and this was observed independently from the treatment (H or H+) and the conditioning time (before or after). In terms of emotional indicators, similar changes in acoustic features of grunts were already found in studies focusing on vocal markers of valence in pig (Briefer et al. 2019; 2022; Avelyne S. Villain et al. 2020a; Friel et al. 2019)and are also in line with previous results in similar contexts in relation to the human presence (Avelyne S. Villain et al.

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2020b). These results, combined with the behavourial results, validate the vocal parameters encoding of positive emotions in the context of a reunion with a human.

In addition, and surprisingly, tamed piglets produced shorter grunts than untamed piglets whatever the context of observation (with or without human presence). This was previously shown in another context (anticipation of (pseudo)social events independently from the type of partner) in the same groups of pigs (Villain et al. 2020). This may show that taming modulates general vocal production in pigs on a long term.

We showed that the proximity to the human changed the structure of piglets grunts and that proximity significantly interacted with the treatment and the conditioning time. Indeed, similarly to a previous study (Villain et al. 2020a, 2020b), during the standard reunion test (no contact from the human), piglets produced shorter and higher pitched grunts with an upshifted frequency spectrum when closer to the human. It was especially the case in untamed piglets and before the conditioning. These results may be linked to the reactivity to the human, untamed piglets being more reactive to the presence of a human. Indeed, before the sessions of the conditioning, tamed piglets were habituated to a human interacting positively when present whereas untamed piglets were not, hence, during the first standard reunion test, when the human is present but do not interact with the piglet, tamed and untamed piglets may have diverging expectations regarding the presence of the static and silent human. As tamed piglets received positive contacts everytime they were in the presence of the human, they may have expected contacts when approaching her and experienced an absence of reward during the test. This has already been hypothetised in piglets deprived from human voice during interactions after a period of habituation to it (Bensoussan et al. 2020). Untamed piglet on the contrary never experienced additional positive contacts and being close to the human, having the possibility to investigate her may be some kind of reward after the period of total isolation. After the conditioning, piglets both treatments were conditioned to receive additional positive contacts and both groups had experienced a first standard reunion test, so they may both experience an absence of reward during the test to some degree, which may explain a lower reaction to proximity to the human, and thus fewer changes on grunt spectro temporal features.

The results on vocal expression during the standard reunion test show that even in a context in which the human does not provide positive contacts, the experience the piglets previously had with her affected their vocal expression when close to her and on the long term. On the one hand, we know a positive HAR establishes through successive positive experiences (Rault et al. 2020) (Rault et al. 2020) and, on the other hand, HAR may have long term effects on behavioural expressions, as

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suggested by Brajon et al. (2015) using cognitive bias tests. We can thus hypothesize this may also be reflected in the way piglets vocally express. In that case, we may have evidence of expression of another category of affect, moods, and not only emotional expression. Indeed, as suggested by Schnall (2010), although emotions are short term affects triggered by an external stimulus, moods, on the other hand may be experienced on a longer term and may not be attribuable to a specific stimulus. Although emotions and moods do not express on the same time scale they may interact with one another and more studies need to be carry out to disantangled their effects on vocal expression.

However, this test led to two potential hypotheses to explain why effect of human proximity on grunt acoustic parameters attenuated as the familiarity to the human increased (decreasing in reactivity along with increasing in foraging natural behaviours or violation of piglets expections with a static human, inhibiting vocal reactions to the proximity). The interpretation of the second type of human-piglet interactions may allow to address these hypotheses.

Providing rewarding additional positive contacts changes the structure of grunts

During the sessions of additional positive contacts of the conditioning, independently from the trial number, the duration of grunts was lower when the piglets were located close to the human and similarly short in both experimental treatments, but when away from the human, untamed piglets had longer grunts than tamed piglets. In addition, although the pitch (AcPC2) and the frequency distribution (-AcPC1) increased over the conditioning, it remained higher when grunts were produced closer to the human and especially in untamed piglets (AcPC2). These results are in line with the behavioural results showing an increase in proximity to the human over the conditioning (CondPC1). During this type of interaction, and contrary to the standard reunion test, changes in acoustic features of grunts when close to the human were consistent over the conditioning: piglets remained reactive to the proximity to the human over time. This result may not be in line with the first hypothesis : in the case of a human interacting with a piglets, the effect of the proximity does not seem to attenuate over time. Hence, the behaviour of the human during a session impacts the way a piglet vocalises. In that case, we may raise two more hypotheses to explain this vocal behaviour : either it is linked to the emotional state or it is linked to a specific human-animal communication, the two explanations may not be exclusive. The first possible explanation may be linked to the emotional state experienced by the piglets when approaching a human providing additional positive contact. As a reminder, in the context of the session, the piglet can chose to approach and stay close to the human, which will provide positive contacts systematically. So the piglet may anticipate to receive

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positive contact and systematically being rewarded. When close to the human, observed changes in frequency distribution of grunts (increased pitched and up shifted frequency spectrum) are known to be markers of arousal (in multiple mamalian species (Briefer 2012; 2020) and pigs (Linhart et al. 2015)). As a consequence, this may show that piglets enter a state of higher arousal when being close to a carying human. To go furhter, we show that these spectral changes were also associated with shorter grunts. Although the duration of grunts is associated to the valence of a situation, it is not clear whether the duration could also be an indicator of the arousal, if our hypothesis is true then it would be the first demonstration that shorter grunts are also indicators of higher arousal positive state in pigs. Last, we can raise the question whether changes in grunt structure may also be associated to a specific human-piglet communication. In other domestic species, owner directed vocalisations has been shown (in cats, reviewed in (Turner 2017); in dogs (Gaunet, Savalli, and Legou 2022)). In addition, paraleles studies have found similar socio-communicative behaviours toward a human in socialized pigs and dogs (Gerencsér et al. 2019). Hens, we may profit from testing the existence of human directed vocalisations in pigs, as consequences of their socio communicative abilities.

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

We found that the identity of the human had effects on behavioural and vocal parameters. Piglets tamed by the human 'AH' had higher values of behavioural proximity (ReuPC1) than piglets tamed by the human 'AV' during reunion test after a period of isolation. This effect was not found during conditioning sessions. Additionally, when the human 'AH' was in the room, piglets produced grunts with a more upshifted frequency spectrum and a higher pitch than when the human 'AV' was in the room, leading to the conclusion that 'AH' was more entitled to trigger higher positive states than 'AV'. Interestingly, the effect of spatial proximity depending the identity of the human on piglets grunts was found during the sessions of additional positive contacts but not when the human was static during the standard reunion test. Hence, it is possible that the way one human interact (behavioural and vocally) with a piglet may be more or less effective at triggering positive emotions and thus modifications of grunt structure. Several evidence exist in the literature that pigs discriminate humans visual and auditory cues (Brajon et al. 2015c; Bensoussan et al. 2019). Pigs may also show behavioural changes hearing human voice (Bensoussan et al. 2020). We may question the efficiency of different human features to generate a positive HAR. In our study, both humans that interacted with the piglets wear exactly the same clothes and standardized their tactile interactions toward the piglets before starting the study, and agree on the rhythm and types of sounds (the words used) to use, to minimise generating variability although no systematic controls of the human

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behaviour or spectral feature of voices were performed here. It thus remains unclear whether experimenters interacted diffently or if they were initially perceived differently by piglets. Studies of human features that are most likely to generate a positive HAR may be of interest regarding animal welfare. In addition, studying human-pig relationship in a more systematic way, as in other domestic species with example of play behaviour in dogs (Horowitz and Hecht 2016) or the acoustic example of the pet directed speech (Lansade et al. 2021; Jeannin et al. 2017), may shed light on the evolution and converging strategies of interspecific relationships. However, the influence of human identity did not modify the general outcomes of our study, but only decrease some effects, suggesting that this variability does not modify the main results, but should be considered in future studies.

To conclude, we showed that degrees of familiarity toward a human could be reflected in the way piglets vocalise in their presence, and out of it. We also showed that the spatial proximity toward a human providing additional care could change the acoustic structure of piglet grunts. These changes are likely to be linked to positive and more intense emotional states that when piglets are further away from the human. However, it is still unclear whether the changes in grunt structure could also be linked to human-animal communication and more studies are needed to determine it. We did also show that the identity of the human may be of important, generating specific vocal changes during additional positive contacts that were not associated to changes in behaviour. More systematic studies of human behaviour along with pig behaviour during the human-animal interactions would be needed to have a better understanding of the evolution of HAR, especially interactive interspecific communicaiton as well as providing new procedures to promote positive welfare. We suggest that the use of vocalisations to assess quality of human-pig relationship could help to better monitor the parameters involved in the establishment and maintenance of a positive HAR.

Authors contributions

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

Acknowledgments

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We acknowledge all the technical staff at UEPR: especially Patrick Touanel and Marie-Hélène Lohat, who largely participated in handling the piglets. We thank Eric Siroux who helped building the acoustic chamber at the beginning of the experiment and Remi Resmond for great discussions about statistics. This project is part of the SoundWel project in the framework of the Anihwa Eranet and funded by ANR 30001199.

Data availability

The datasets used and/or analysed during the current study are available at (Villain et al. 2022).

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618 # References

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