Early vocal ontogeny in a polytocous mammal: no evidence of social learning among sibling piglets, *Sus scrofa*

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A R T I C L E   I N F O

Animals living in social proximity often have similar vocalizations. For many bird and several mammal species, at least part of the vocal similarity is socially learned during ontogeny. Little is known, however, about the ontogenetic origin of vocal similarities among siblings in polytocous mammals. We investigated the influence of social environment and genetic relatedness on the development of acoustic similarities among suckling piglets. To examine whether the common acoustic features are innate or learned by postnatal vocal convergence in the same litter, we cross-fostered piglets among pairs of mother sows immediately after birth and recorded contact calls (grunts) of both the cross-fostered and the noncross-fostered piglets during the suckling period. Acoustic distances of the cross-fostered piglets to their new littermates remained longer than those among noncross-fostered siblings and were as long as those between piglets from different litters. The results show that after being neonatally cross-fostered to another litter, the piglets did not converge acoustically with their new littermates even after several weeks of cohabitation. This is in contrast to the presence of vocal plasticity during the ontogeny of other mammals including other ungulates, indicating that use of vocal learning may vary even in closely related species, perhaps in relation to its adaptive utility within the life history and social organization of the species.

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Group-living bird and mammal species use vocalizations extensively for intraspecific communication. Besides information about external events such as danger (Barati & McDonald, 2017; Chan, Cloutier, & Newberry, 2011; Zuberbühler, 2009) or food (Clay, Smith, & Blumstein, 2012; Evans & Evans, 1999), internal states such as fear (Barros & Tomaz, 2002; Düpjan, Schön, Puppe, Tuchscherer, & Manteuffel, 2008), pain (Prunier et al., 2013; Puppe, Schon, Tuchscherer, & Manteuffel, 2005), sex of the caller (Rubow, Cherry, & Sharpe, 2017a) or general emotional valence/arousal (Burgdorf et al., 2008; Lindová; Špinka, & Nováková, 2015; Linhart, Ratcliffe, Reby, & Špinka, 2015; Reimert, Bolhuis, Kemp, & Rodenburg, 2013) and motivations/intentions (McGrath, Dunlop, Dwyer, Burman, & Phillips, 2017), vocalizations can also contain cues about individual and/or group identity. Interindividual differences in vocalizations exist in different forms both in birds and in mammals (Boughman & Moss, 2002; Catchpole & Slater, 2008; Sheehan, Miller, & Reeve, 2017), ranging from specifically designed 'signature' calls that are individually distinctive (King et al., 2018; Luis, Couchinho, & dos Santos, 2016; Mumm, Urrutia, & Knornschild, 2014; Sayigh & Janik, 2018; Toth & Parsons, 2018) to subtle differences in common call types such as contact calls (Farabaugh, Linzenbold, & Dooling, 1994; Salmi, Hammerschmidt, & Doran-Sheehy, 2014; Sewall, Young, & Wright, 2016; Weary & Krebs, 1992), that may be sufficient for reliable individual recognition (D'Amelio, Klumb, Adreani, Gahr, & ter Maat, 2017; Terleph, Malaivijitnond, & Reichard, 2015). Calls can also be more similar between members of the same group than they are between individuals belonging to different groups (Boughman & Wilkinson, 1998; Nowicki, 1983; Tyack, 2008) thus supporting group membership recognition (Price, 1999).

One example of group recognition is vocal similarity between siblings from the same litter or clutch. Sibling vocal similarity has so

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far been investigated mainly in birds (Dreiss, Ruppli, & Roulin, 2014; Ligout, Dentressangle, Mathevon, & Vignal, 2016; Nakagawa & Waas, 2004; Sharp & Hatchwell, 2006; Wanker, Apcin, Jennerjahn, & Waibel, 1998) and in several monotocous mammals that occasionally give birth to twins or triplets (Briefer & McElligott, 2012; Knornschild, Von Helversen, & Mayer, 2007; Masters, Raver, & Kazial, 1995). To our knowledge, sibling vocal similarity has not yet been studied in any polytocous mammals. Few studies have investigated the ontogenetic mechanisms, either through cross-fostering or another method, by which similarity between sibling voices arise (Dreiss et al., 2014; Reers, Leonard, Horn, & Jacot, 2014; Stuart P. ; Sharp, McGowan, Wood, & Hatchwell, 2005), which is in contrast to much more advanced knowledge in the olfactory realm (e.g. Mateo, 2003).

Both interindividual and intergroup differences in vocalizations may originate through an interplay of source (vocal folds capable of vibration) and filter (differently shaped vocal tract above the folds) components in vocal production (Taylor & Reby, 2010; Tokuda, 2018). Both these components can be affected by genetic differences, prenatal environment, common/different postnatal physical environment and/or differential growth/maturation effects. Furthermore, vocal production learning may produce individual signatures that are based on differences in the signal itself rather than on differences in vocal tract morphology (Janik & Sayigh, 2013). Vocal similarities in animal groups can also arise through social learning during postnatal/posthatching ontogeny (Arriaga & Jarvis, 2013; Janik & Slater, 2000; Knornschild, Nagy, Metz, Mayer, & Von Helversen, 2012; Medvin, Stoddard, & Beecher, 1992; Nowicki, 1983; S. P. ; Sharp & Hatchwell, 2006). Vocal imitation, that is, social learning of new vocalization types from tutors, is widespread among birds, particularly among hummingbirds, parrots and songbirds. In mammals, learning of new vocalization types seems to be less frequent, so far being documented in humans, cetaceans (Eaton, 1980), bats (Knornschild, Nagy, Metz, Mayer, & von Helversen, 2010), seals (Ralls, Fiorelli, & Gish, 1985) and elephants (Stoeger & Manger, 2014). However, since mammals tend to have more continuous repertoires (Hammerschmidt & Fischer, 1998; Keenan, Lemasson, & Zuberbuhler, 2013; Tallet et al., 2013; Yin & McCowan, 2004), they may have another type of vocal social learning, namely vocal convergence or accommodation (Ruch, Zurcher, & Burkart, 2018; Tyack, 2008). In contrast to vocal imitation, vocal convergence does not include acquisition of new call types, motifs or themes but rather proceeds by changing the acoustic characteristics of an existing call type so that the vocal expression becomes more similar among group members (Knornschild et al., 2012). Briefer and McElligott (2012) documented a case of within-group vocal convergence among 23 goat, *Capra hircus*, kids housed in four groups during their first 5 weeks of life. This was the first evidence of vocal convergence in an ungulate species and one of the very few mammal species in which social vocal learning has been examined in early ontogeny (Knornschild et al., 2012), most research on social vocal learning having focused on vocalizations produced at later stages of life. Briefer and McElligott (2012) speculated that similar vocal plasticity could be present in many other mammals but has gone undetected. We therefore examined whether vocal convergence exists in another highly vocal and social ungulate species, the domestic pig. Litter identity information is known to be present in the grunt vocalization of suckling piglets (Illmann, Schrader, Špinka, & Šustr, 2002; Syrová, Policht, Linhart, & Špinka, 2017). In the current study, we used the powerful tool of cross-fostering (McCarty, 2017) to establish whether the vocal similarity between young sibling piglets is innate or socially learned. Vocal similarity may be expressed differently in different situations (Mitani, Gros-Louis, & Macedonia, 1996; Rubow, Cherry, & Sharpe, 2018; Syrová et al., 2017) and thus

the cross-fostering may affect calls produced in different contexts in various ways. Therefore, we recorded the piglet calls in two situations: short-term isolation and manual restraint in the form of a standardized back test (Hessing et al., 1993). These two situations were chosen for two reasons. First, they have been repeatedly used in the study of piglet emotionally loaded behaviours (Illmann et al., 2002; Leliveld, Düpjan, Tuchscherer, & Puppe, 2017; Linhart et al., 2015; Scheffler, Stamer, Traulsen, & Krieter, 2014; Zebunke, Nürnberg, Melzer, & Puppe, 2017) making it possible to interpret the results of the current study in the light of existing knowledge. Second, the two tests mimic natural fitness-threatening situations that could occur to young free-living piglets, namely, losing visual contact with the mother and other group mates in the dense forest environment and being trapped next to the body of a larger conspecific during communal resting or nursing.

We aimed to test the following specific hypotheses: (1) calls of piglets cross-fostered into another litter shortly after birth will become more similar to those of their new littermates and more dissimilar to those of their biological siblings; (2) these effects will become more pronounced with time spent in the new litter; and (3) the strength of the acoustic identity signal (both at the individual and at the litter level) will be different in the two situations that differ in adversity and in possible adaptive value of the vocal signalling, namely in isolation and in restraint.

METHODS

Ethical Note

The experiment was conducted in accordance with Czech laws and regulations and with approval of the Ethic Committee of the Institute of Animal Sciences in Prague. The research was performed under accreditations 60444/2011-MZE-17214 and 18480/2016-MZE-17214 and a licence permitting experimentation with animals for Marek Špinka. Piglet manipulation during both the isolation and back test was within limits of regular husbandry procedures.

Animals

We tested 153 (Large White × Landrace) × (Duroc × Pietrain) piglets from 28 litters (minimum of four piglets per litter). Piglets were marked by unique ear tags and we also noted their sex and weight. The experiments were conducted at the Netluky pig farm owned by the Institute of Animal Science in Prague (Czech Republic) in 2014–2016. Mother sows were housed in standard 2.3 × 2 m farrowing pens equipped with sow crates and positioned in the same farrowing room. The sows were provided with ad libitum lactating sow feed and water while the piglets had continuous access to a heated nest, creep formula feed (starting from day 10 of life) and a nipple drinker.

Experimental Design

The design of our experiment was based on 14 pairs of synchronized litters born within 24 h of each other. Median litter size was 11.5, the interdecile range was 9–14 piglets and the range 6–16 piglets. Within each litter pair, two piglets from each litter were switched between 12 and 24 h after birth. These piglets were approximately average weight for the given litter and were marked by an ear tag of different colour. After the cross-fostering we monitored the behaviour of sows for occurrence of aggressive behaviour against piglets, but no such behaviour was observed in any litter.

Recordings

We recorded piglet vocalizations first within 4 days after cross-fostering (Week 1, median age 4, range 3−5 days) and then just before weaning (Week 4, median Week 46, range 23−41 days). Recordings were conducted in a separate room (with no other animals present) during two situations: isolation and a back test. The tested piglet was placed in a wooden box (0.5 × 0.5 × 0.5 m) and audio-recorded in isolation for 2 min. Thereafter, we conducted the back test by putting the piglet on its back and restraining it manually in the supine position on a flat surface for 1 min. The recorder (Olympus Linear PCM recorder LS-12, frequency response 20 hz−21 kHz) was placed 1 m above the floor of the isolation box and during the back test 1 m from the piglet's snout. Immediately after recording, the piglet was returned to the sow and littermates.

Because of an organizational failure at the experimental farm and health issues in two of the 28 sows, three pairs of litters containing 35 experimental piglets dropped out of the experiment before Week 4. Of the 118 remaining experimental piglets in 11 litter pairs, six died or fell ill by the recording day at Week 4. The drop-out rate was similar in cross-fostered piglets (two of 37, i.e. 5%) and in noncross-fostered piglets (four of 81, i.e. 5%) and corresponded to the usual combined mortality plus morbidity rate of piglets between 1 and 4 weeks of life in the herd. As a result of these events, the number of recorded piglets was 150 for isolation at Week 1, 152 for the back test at Week 1, 114 for isolation at Week 4 and 115 for the back test at Week 4.

Acoustic Analysis

The study focused on grunt calls, that is, contact calls that piglets produce in a number of situations (Tallet et al., 2013) and that could be easily distinguished by having most of their energy below 1 kHz (Fig. 1). In both the isolation and the back test situation, we selected 10 grunts per individual that did not overlap with any other noise such as hoof tapping. In some recordings, fewer than 10 good-quality grunts were available. We edited the selected grunts manually and saved them as separate spectrograms using Avisoft SAS Lab Pro (Avisoft Bioacoustics, R. Specht, Berlin, Germany) with the following settings: FFT length 1024,
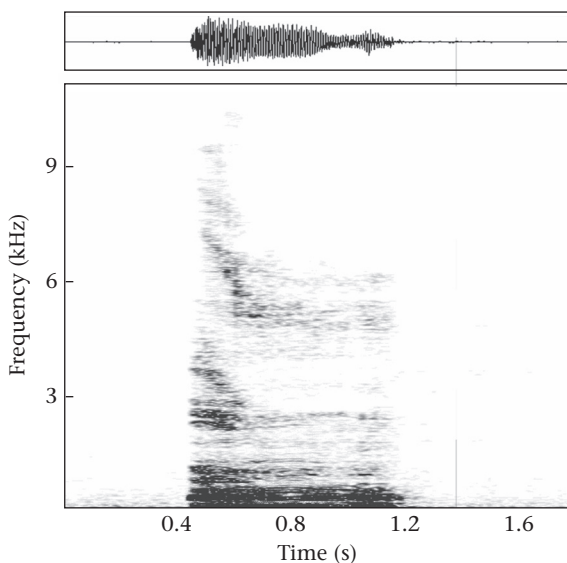
Figure 1. Oscillogram (top) and spectrogram (bottom) of a typical grunt produced by a piglet at the age of 5 days.

overlap 87.5%, frame size 100%, Hamming window, time resolution 2.9 ms. The spectrograms were then analysed both in Avisoft (four acoustic parameters extracted) and in LMA 2008 software (provided by K. Hammerschmidt, 116 acoustic parameters extracted, see Appendix Table A1).

Statistical Analysis

To develop a classification of grunts according to the identity of the piglet producing them, we used a stepwise discriminant function analysis (DFA). We first reduced the number of acoustic parameters to 10, following the rule that the number of parameters included in the DFA should not exceed the number of samples per individual (Mundry & Sommer, 2007). The selection of acoustic parameters proceeded as follows. First, parameters that either had zero variation or were highly intercorrelated ($r > 0.9$) were excluded (McGarigal, Cushman, & Stafford, 2000). After this step, 47 variables remained for isolation at Week 1, 80 variables for isolation at Week 4, 91 variables for the back test at Week 1 and 87 variables for the back test at Week 4. Then, one-way analyses of variance (ANOVAs) with piglet identity as the explanatory variable were conducted and the 10 acoustic variables with the highest *F* values were selected for DFA (Appendix Table A2). These variables were selected separately for each of two age classes and both contexts (isolation, back test). This was done to ensure we always used the optimal combination of parameters as it is known that in different situations, different parameters have the best potential to distinguish between individuals (Rubow et al., 2018). Thus, we conducted four separate DFAs: isolation at Week 1, isolation at Week 4, back test at Week 1 and back test at Week 4. Classification results of DFA were validated using the leave-one-out cross-validation procedure (IBM SPSS Statistics 20, IBM, Armonk, NY, U.S.A.). The vocal similarity of grunts among the piglets was quantified through pairwise distances generated from each independent DFA. The acoustic distances were log transformed to improve normality.

Statistical testing was performed using SAS 9.4 software (SAS Institute Inc., Cary, NC, U.S.A.). The overview and the description of the statistical models are given in Appendix Table A3. Linear mixed models with variance components, covariance structure and identity link function were used. All the models were checked for normality of residuals and normality of random factor estimates through normal probability plots and for homoscedasticity through plotting the residuals against the individual fixed effects.

The statistical testing started with three preliminary analyses before proceeding to the main tests of the three core hypotheses. In preliminary analyses, we first checked whether the cross-fostering procedure itself affected body weight and/or changed the acoustic parameters, using linear mixed models (one model for each parameter, with litter as a random factor) that contrasted the fostered piglets against piglets that remained in their native litters. Next, we assessed, also through a linear mixed model, whether differences in weight and/or sex affected the acoustic distance between piglet dyad grunt calls.

In the main analysis, we tested hypotheses 1, 2 and 3. A linear mixed model was calculated, with the response variable being the mean acoustic distance for each piglet in each of the four classes of dyads. The fixed effects were the dyad class (with four levels), age (two levels) and test situation (two levels). The four dyad classes are depicted in Fig. 2 and were defined as follows: Own-Own = both piglets born in the same litter and stayed there; Own-OutF = both piglets born in the same litter, one of them cross-fostered to the other sow in the sow pair; Own-Alien = each piglet born to a different litter and stayed in that litter; and Own-InF = one piglet born and stayed in a litter, the other in-fostered to that litter after
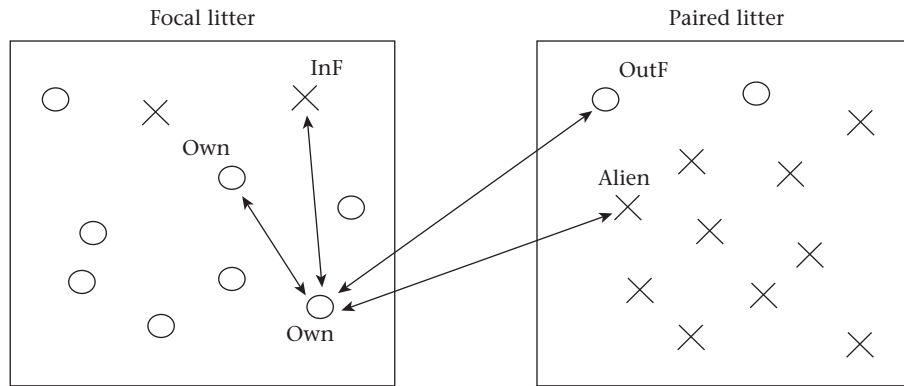
Figure 2. Scheme depicting the cross-fostering design and the four classes of acoustic distances between piglet dyads that were measured in the experiment. Circles denote piglets born in the focal litter, crosses stand for piglets born in the other litter of the sow pair. For each litter, four types of piglets were distinguished: Own piglets were born and stayed in the focal litter; OutF piglets were born in the focal litter and were neonatally cross-fostered to the other litter; Alien piglets were born and stayed in the other litter; and InF piglets were cross-fostered to the focal litter after being born in the other litter.

being born to the other sow. All interactions between fixed effects were included in the model. Piglet identity and litter identity entered the models as random effects. After finding an overall significant effect of the dyad class, we performed preplanned pairwise comparisons, testing whether the Own-Own distance differed from any of the Own-OutF, Own-Alien or Own-InF distances and whether Own-InF distances differed from Own-Alien distances.

RESULTS

Effect of Moving Piglets Between Litters

The piglets that underwent the cross-fostering procedure did not differ in weight from those that remained in the native litters (mixed model: $F_{1,109} = 1.55$, $P = 0.213$). In addition, values of the 40 vocal parameters (10 parameters per situation and age) did not differ between piglets that underwent the cross-fostering and piglets that remained in natal litters (40 univariate mixed models, 39 mixed models with $P > 0.1$, one model with $P = 0.043$). Therefore, we concluded that neither the piglets' physical state nor their vocal quality was systematically changed by the cross-fostering procedure itself.

Effects of Weight and Sex Differences

The acoustic distance between two piglets was not significantly affected by their weight difference ($F_{1,2260} = 3.68$, $P = 0.055$). In addition, sex had no significant influence on the acoustic distance of a given piglet dyad ($F_{1,2260} = 1.86$, $P = 0.173$).

Effects of Social Environment

In the main analysis, hypothesis 1 was tested by focusing on the effect of dyad composition on the acoustic distances. The mixed model revealed that acoustic distance between two piglets was affected by the composition of the dyad (Fig. 3; mixed model: $F_{3,1320} = 7.65$, $P < 0.001$; see also Fig. A1 in the Appendix for an illustration of the spread of the data). The pairwise comparisons showed that Own-Own distances were shorter than Own-Alien distances ($t_{1320} = 4.15$, $P < 0.001$), Own-InF distances ($t_{1320} = 4.14$, $P < 0.001$) and Own-OutF distances ($t_{1320} = 2.92$, $P = 0.004$). Critically for hypothesis 1, Own-InF distances were not shorter than the Own-Alien distances ($t_{1320} = 0.01$, $P = 0.991$).

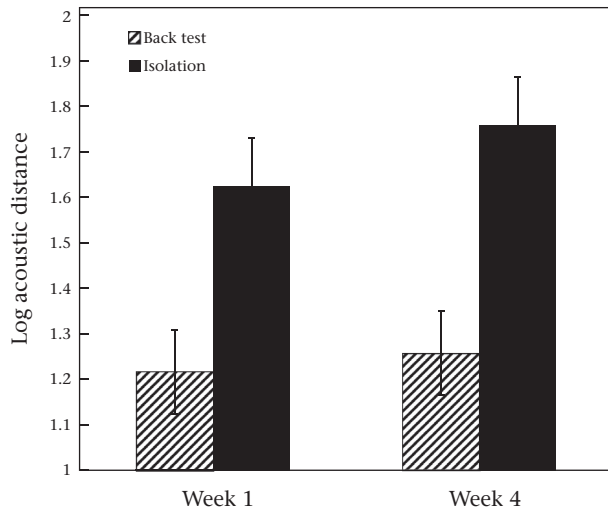### Effects of Age and Situation

The mixed model also assessed hypotheses 2 and 3 by focusing on the effects of age and test situation on acoustic distances (Fig. 4). The acoustic distances increased slightly but significantly between Week 1 and Week 4 ($F_{1,1320} = 4.98$, $P = 0.026$). Importantly for hypothesis 2, none of the interactions including the age effect was significant (age*dyad class: $F_{3,1320} = 1.22$, $P = 0.300$; age*situation: $F_{1,1320} = 1.66$, $P = 0.213$; age*situation*dyad class: $F_{3,1320} = 0.19$, $P = 0.906$). In agreement with hypothesis 3, the test situation had a strong effect with the distances being larger for isolation grunts than for back test grunts ($F_{1,1320} = 149.59$, $P < 0.001$).

DISCUSSION

Our results do not provide support for social learning as a mechanism through which acoustic litter identity arises in suckling piglets. If social learning led to vocal convergence among piglets growing up in the same litter, then in our experiment the piglets
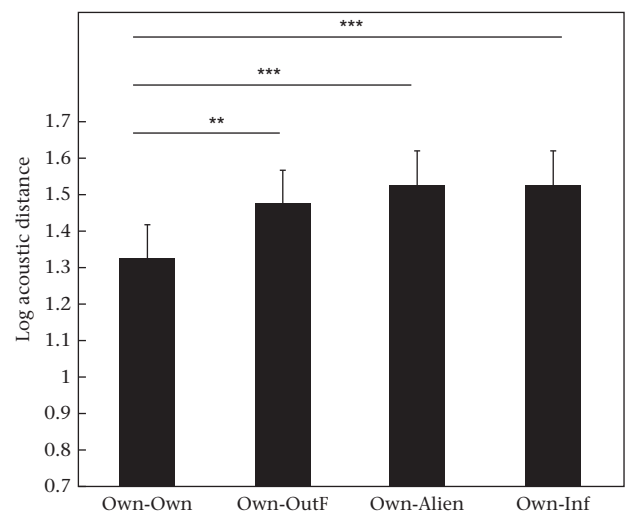
Figure 3. Acoustic distances (least square means + SE) between the four classes: Own = piglets that were born and stayed in the focal litter; OutF = piglets that were born in the focal litter and were fostered neonatally into the other of the two paired litters; Alien = piglets that were born and stayed in the other of the two paired litters; InF = piglets that were in the other of the two paired litters and were fostered neonatally into the focal litter. Significant pairwise differences: **$P < 0.01$; ***$P < 0.001$.

Figure 4. Acoustic distances (least square means ± SE) as influenced by age and test situation. See text for the significance of the two effects.

that had been in-fostered into a non-native litter (InF piglets in our notation) should become gradually more similar in their calls to their new littermates (Own piglets). Thus, the Own-InF acoustic distances should have been shorter than the distances in the 'control' case, i.e. between nonlittermates that stayed in their respective natal litters (Own-Alien distances). However, Own-InF distances were not shorter than the Own-Alien ones. Furthermore, if the within-litter similarity in vocalizations were mainly due to social learning, then piglets in-fostered into a litter immediately after birth should have been almost as close acoustically to their native littermates as the native littermates were among each other, that is, the Own-InF distances should have been nearly as short as the Own-Own distances. Contrary to this prediction, Own-InF acoustic distances were substantially larger than Own-Own distances.

The most plausible explanation for the lack of vocal conformity between the in-fostered piglets and the host litter piglets seems to be that vocal similarity is present at birth in the biological siblings and no vocal accommodation occurs postnatally within the litters. An alternative explanation might be that the social learning capability exists in young piglets, but it was impaired in the cross-fostered piglets by the stress of the transfer between the litters. We cannot exclude this possibility. Nevertheless, our results show that the cross-fostered piglets were not at a disadvantage in terms of milk access as they grew to the same weight as the noncross-fostered piglets. Also, there were no indications of a higher stress level in the vocalizations of the cross-fostered piglets. Increased levels of negative emotional states are known to change acoustic parameters of vocalizations (Briefer, 2012; Giddens, Barron, Byrd-Craven, Clark, & Winter, 2013; Linhart et al., 2015) but we did not find any systematic change in the vocal parameters we examined in cross-fostered as opposed to noncross-fostered piglets. Finally, we designed the experiment so that possible stress was minimized. The piglets were cross-fostered when they were 12–24 h old, before their preference for their own mother versus other lactating sows was fully established (Horrell & Hodgson, 1992) and the mutual switching of piglets between pairs of litters meant that there were free functional teats available for the fostered pigs.

The fact that social learning did not occur does not exclude the possibility of other environmental influences on acoustic characteristics of the calls. If there were no postnatal effects of any kind, and thus the vocal similarities between siblings were fully innate (i.e. solely due to the shared genetics and/or the shared prenatal

environment), then the out-fostered piglets should have remained as similar to their mother-reared siblings as these were among each other. In our case, the acoustic distances should have stayed as short in Own-OutF dyads as they were in Own-Own dyads. However, the Own-OutF distances were longer than the Own-Own distances. This result indicates that when a piglet is fostered into another litter, its vocalization may drift away from the common acoustic characteristics of its litter. Nevertheless, this drifting away does not bring it closer to the acoustic characteristics of its foster social environment, as discussed above. Besides answering the main question about putative social learning of vocal characteristics, the results also showed that the Own-Alien distances were greater than Own-Own distances, thus confirming the previously documented fact (based on 50 acoustic parameters, most of which were also included in our initial parameter set) that the grunts of suckling piglets contain information about litter identity (Illmann et al., 2002).

There was no support in our results for hypothesis 2, that is, for social environment effects becoming stronger with increasing age. If hypothesis 2 were true, then acoustic distances would change differently with time in the different dyad classes, for example Own-InF distances would decrease while the Own-OutF distance would increase. However, neither the age*dyad class interaction nor the age*dyad*situation interaction was significant. Rather we found a significant, albeit weak main effect of age, indicating that the acoustic distances were slowly increasing across lactation among all piglets as already shown by Syrová et al. (2017).

Finally, the acoustic distances between pairs of piglets were greater in isolation than during the back test, thus supporting hypothesis 3. A previous study found that calls from isolation are easier to assign to the correct piglet than calls from the back test (Syrová et al., 2017). Taken together, these results indicate that grunts produced in the isolation situation carry more information about identity (be it the individual identity of the piglet or the common litter identity) than grunts produced in the restraint-inducing back test. A plausible interpretation of this finding is that the vocalizations have slightly different adaptive functions and therefore slightly different acoustic structure in the two situations (cf. Lingle, Wyman, Kotrba, & Romanow, 2012; Rubow et al., 2018; Tallet et al., 2013). In isolation, piglets are trying to re-establish vocal contact with the mother so that she can vocalize back, and they can find the way back to her. In contrast when they are restrained/trapped, they mainly need to elicit help from the mother or another genetically related adult member of the group (Podgorski, Scandura, & Jedrzejewska, 2014) and thus the need to communicate strong negative emotional state may overrule the identity signalling. This interpretation is related to the finding in a playback study (Illmann et al., 2002) that if the reaction of a mother sow to piglet calling is of low intensity (calling back), then she reacts preferentially towards her own progeny's vocalizations whereas in a higher-level physical reaction (moving towards the loudspeaker), the sow does not differentiate between her own and alien piglets. Furthermore, pig grunt vocalizations change their acoustic structure (e.g. by decreasing the signal-to-noise ratio) with increasing negative arousal (Linhart et al., 2015) which may make the detection of individual and/or group identity more difficult in calls produced during the more arousing back test situation. Analogously, Rubow et al. (2018) also found that lower arousal isolation calls by dwarf mongooses, *Helogale parvula*, carry stronger information about caller identity than snake alarm calls.

Our results contrast with the findings of Briefer and McElligott (2012) that vocalizations converge in groups of young goat kids. The two studies are very similar in that they both examined development of a contact call in highly social ungulate species

during the first weeks of life. Both studies focused on establishing the effects of kinship and group/litter membership on convergence, or lack thereof, of acoustic properties of the calls. Our study used a larger sample size (156 piglets in 28 litters compared to 23 kids in four groups in the Briefer & McElligott study). We also employed a more powerful design of cross-fostering while Briefer and McElligott (2012) relied on natural between-group differences and thus the important case of full siblings reared in different social environments was missing in their design. Despite the strong design, we found no evidence for vocal convergence and thus for vocal learning in piglets. The contrasting results, together with other positive (Knornschild et al., 2010, 2012) and negative (Kikusui et al., 2011) findings, indicate that further studies in more species are needed to clarify how widespread vocal learning is among young mammals. Cross-fostering should be widely recommended as a powerful method for disentangling innate from learned contributions to phenotypical similarities between siblings, group mates or genetically different lines of animals (McCarty, 2017). In relation to vocal similarity, the procedure has been applied between different species (Arriaga & Jarvis, 2013; Masataka & Fujita, 1989; Owren, Dieter, Seyfarth, & Cheney, 1993; Pasch et al., 2016), between different genetic strains (Arriaga, Zhou, & Jarvis, 2012; Kikusui et al., 2011; Wöhr et al., 2008) and between different groups (Janette Wenrick Boughman, 1998) but surprisingly rarely between litters of polytocous mammals.

As data from more species become available, it may become possible to address the question whether the ability of early vocal learning is adaptively linked with some aspects of the species' brain evolution (e.g. lateral cerebellar expansion, Smaers, Turner, Gomez-Robles, & Sherwood, 2018), reproductive life history, social organization and/or ecological niche. For instance, vocal learning may have evolved among young nonsibling group mates in monotocous group-living species such as bats (Knornschild et al., 2012), goats (Briefer & McElligott, 2012) or dolphins (Fripp et al., 2005) rather than among siblings of polytocous species such as mice (Kikusui et al., 2011) or pigs (this study). For monotocous group-living mammals, individuals capable of vocal accommodation may be favoured by natural selection because they become more recognizable by their vocal phenotype as members of the group. The accommodation may be selectively advantageous even if the learning process takes some time during ontogeny. In contrast, for mothers of polytocous species, it is important to distinguish between their own progeny and nonfilial young from the moment of birth, and therefore it may be too risky for them to rely on any learning processes in the offspring that would only gradually develop the distinguishing cues or signals. Thus, there might have been little selective pressure in young siblings to develop an acoustic convergence based on social learning. Rather, a swift learning process may have evolved in the polytocous mothers themselves through which they quickly learn the individual contact calls of all the young in the litter. For the domestic pig, there is evidence for such a process in the olfactory realm: a cross-fostering experiment indicated that postparturient sows quickly (within 24 h postpartum) 'imprint' all the individual scent signatures of their numerous newborn young rather than identifying them through a shared scent derived from the milk or the shared nest (Maletínská; Špinka, Víchová, & Stěhulová, 2002). In the acoustic realm, mother sows are also able to react preferentially to their own progeny's vocalization (Illmann et al., 2002). Whether this is based on recognition of acoustic profiles of individual piglets or on acoustic characteristics that are shared among littermates will only be established by carefully designed playback experiments.

In conclusion, this is the first study examining the ontogenetic origin of vocal sibling similarities in a polytocous mammal. No evidence for social learning in the form of vocal accommodation among littermate piglets was found. Rather, the vocal similarities among littermates seem to be present immediately after birth. To better understand the phylogenetic distribution, ontogenetic mechanisms and adaptive functions of social vocal learning, further studies on between-individual similarities and differences in vocalizations are needed in species with different life histories and phylogenetic backgrounds.

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Appendix

Table A1
Acoustic parameters extracted from call spectrograms

Acoustic parameters	Parameter description
AVISOFT software	
Duration (ms)	Duration of the signal
Quartile 25% (Hz)	Below this frequency is 25% of the total energy
Quartile 50% (Hz)	Below this frequency is 50% of the total energy
Quartile 75% (Hz)	Below this frequency is 75% of the total energy
LMA 2008 software	
q1st (Hz)	Start frequency 1st DF
q1end (Hz)	End frequency 1st DF
q1max (Hz)	Maximum frequency 1st DF
q1min (Hz)	Minimum frequency 1st DF
q1mean (Hz)	Mean frequency 1st DF
q1med (Hz)	Median frequency 1st DF
q1maloc	Location of the maximum frequency 1st DF [(1/duration) × location]
q2st (Hz)	Start frequency 2nd DF
q2end (Hz)	End frequency 2nd DF
q2max (Hz)	Maximum frequency 2nd DF
q2min (Hz)	Minimum frequency 2nd DF
q2mean (Hz)	Mean frequency 2nd DF
q2med (Hz)	Median frequency 2nd DF
q2maloc	Location of the maximum frequency 2nd DF [(1/duration) × location]
q3st (Hz)	Start frequency 3rd DF
q3end (Hz)	End frequency 3rd DF
q3max (Hz)	Maximum frequency 3rd DF
q3min (Hz)	Minimum frequency 3rd DF
q3mean (Hz)	Mean frequency 3rd DF
q3med (Hz)	Median frequency 3rd DF
q3maloc	Location of the maximum frequency 3rd DF [(1/duration) × location]
df1st (Hz)	Start frequency 1st DFB
df1end (Hz)	End frequency 1st DFB
df1max (Hz)	Maximum frequency 1st DFB
df1min (Hz)	Minimum frequency 1st DFB
df1mean (Hz)	Mean frequency 1st DFB
df1med (Hz)	Median frequency 1st DFB
df1chfre	No. of changes between original and floating average curve (LM) 1st DFB
df1chmea (Hz)	Mean deviation (LM) 1st DFB
df1chmax (Hz)	Maximum deviation (LM) 1st DFB
df1pr (%)	Percentage of time segments where a 1st DFB could be found
df1maloc	Location of the maximum frequency 1st DFB [(1/duration) × location]
df1miloc	Location of the minimum frequency 1st DFB [(1/duration) × location]
df1trfak	Factor of linear trend 1st DFB (global modulation)
df1fretr	Alternation frequency between 1st DFB and linear trend
df1mintr (Hz)	Minimum deviation between 1st DFB and linear trend
df1maxtr (Hz)	Maximum deviation between 1st DFB and linear trend
DFB2st (Hz)	Start frequency 2nd DFB
DFB2end (Hz)	End frequency 2nd DFB
DFB2max (Hz)	Maximum frequency 2nd DFB
DFB2mean (Hz)	Mean frequency 2nd DFB

Table A1 (*continued*)

Acoustic parameters	Parameter description
DFB2med (Hz)	Median frequency 2nd DFB
DFB2pr (%)	Percentage of time segments where a 2nd DFB could be found
DFB3mean (Hz)	Mean frequency 3rd DFB
DFB3med (Hz)	Median frequency 3rd DFB
DFB3pr (%)	Percentage of time segments where a 3rd DFB could be found
DFB4pr (%)	Percentage of time segments where a 4th DFB could be found
diffmax (Hz)	Maximum difference between 1st & 2nd DFB
diffmean (Hz)	Minimum difference between 1st & 2nd DFB
diffremax	Maximum number of DFBs
diffremin	Minimum number of DFBs
diffreq	Mean number of DFBs
ampratio1	Amplitude ratio between 1st & 2nd DFB
ampratio2	Amplitude ratio between 1st & 3rd DFB
ampratio3	Amplitude ratio between 2nd & 3rd DFB
f1mean (Hz)	GFP
f2mean (Hz)	2nd GFP
f1wst (Hz)	Start frequency 1st GFP
f1wend (Hz)	End frequency 1st GFP
f1wmax (Hz)	Maximum frequency 1st GFP range
f1wmin (Hz)	Minimum frequency 1st GFP range
f1wmean (Hz)	Mean frequency 1st GFP range
f1wmed (Hz)	Median frequency 1st GFP range
fp1max (Hz)	Maximum frequency 1st GFP
fp1mean (Hz)	Mean frequency 1st GFP
fp1amax (relative amplitude)	Maximum amplitude 1st GFP
fp1amean (relative amplitude)	Mean amplitude 1st GFP
f2pr (%)	Percentage of time segments where a 2nd GFP could be found
f2wmean (Hz)	Mean frequency 2nd GFP
f3pr (%)	Percentage of time segments where a 3rd GFP could be found
ranmax (Hz)	Maximum frequency range
ranmean (Hz)	Mean frequency range
ranmin (Hz)	Minimum frequency range
pfst (Hz)	Start PF
pfend (Hz)	End PF
pfmax (Hz)	Maximum PF
pfmin (Hz)	Minimum PF
pfmean (Hz)	Mean PF
pfmed (Hz)	Median PF
pftotmax (Hz)	Frequency of the total maximum amplitude
pftomin (Hz)	Frequency of the total minimum amplitude
pfmaloc (Hz)	Location of the maximum PF [(1/duration) $\times$ location]
pfjump (Hz)	Maximum difference between successive PFs
pftrfak	Factor of linear trend of PF (global modulation)
pftrfre	Alternation frequency between PF and linear trend
Pftrmean (Hz)	Mean deviation between PF and linear trend
pftrmax (Hz)	Maximum deviation between PF and linear trend
csmean	Mean correlation coefficient of successive time segments
csmaxd	Standard deviation of correlation coefficient of successive time segments
csmaloc	Location of maximum correlation coefficient of successive time segments [(1/duration) $\times$ location]
F0start (Hz)	Start frequency F0
F0min (Hz)	Minimum frequency F0
F0mean (Hz)	Mean frequency F0
F0med (Hz)	Median frequency F0
noise (%)	Percentage of noisy time segments
disturb (%)	Percentage of disturbed time segments
tonal (%)	Percentage of tonal time segments
tonalF0 (%)	Percentage of tonal time segments where it is possible to estimate F0
diffmean (Hz)	Mean difference between F0 & PF
diffmax (Hz)	Maximum difference between F0 & PF
diffmin (Hz)	Minimum difference between F0 & PF
amprat1	Amplitude ratio between F0 & 1st harmonic
amprat2	Amplitude ratio between F0 & 2nd harmonic
amprat3	Amplitude ratio between 1st & 3rd harmonic
meanhnr	Mean harmonic to noise ratio (1 = no noise)
maxhnr	Maximum harmonic to noise ratio (1 = no noise)

DF: distribution of frequency amplitude; DFB: dominant frequency band; LM: local modulation; GFP: global frequency peak; PF: peak frequency; F0: fundamental frequency.

Table A2
Acoustic parameters used in the four cross-validated discriminant function analyses (DFAs)

Acoustic parameter		Isolation test		Back test	
		Week 1	Week 4	Week 1	Week 4
General parameters (basic energy distribution)					
q1min	Minimum frequency 1st DF		X		X
q1mean	Mean frequency 1st DF		X		
q1med	Median frequency 1st DF	X			
q2min	Minimum frequency 2nd DF	X			
q2mean	Mean frequency 2nd DF	X			
q2start	Start frequency 2nd DF			X	
q3min	Minimum frequency 3rd DF			X	
q3max	Maximum frequency 3rd DF				X
q3med	Median frequency 3rd DF				X
q3end	End frequency 3rd DF			X	
df2med	Median frequency 2nd DFB				X
df1pr	Percentage of time segments where a 1st DFB could be found		X		X
df2pr	Percentage of time segments where a 2nd DFB could be found				X
df1chmea	Mean deviation of LM 1st DFB				X
df1chfre	No. of changes between original and floating average curve LM 1st DFB				X
fp1amean	Mean amplitude 1st P	X		X	
fp1amax	Maximum amplitude 1st P		X		
csmean	Mean correlation coefficient of successive time segments	X	X	X	X
csmaxd	SD of correlation coefficient of successive time segments	X		X	
quart75	Below this frequency is 75% of energy	X			X
ranmin	Minimum frequency range	X			
Tonal parameters (autocorrelation algorithm describing the tonality)					
hnr	Harmonic to noise ratio	X	X	X	
meanhnr	Mean harmonic to noise ratio		X		
tonalF0	Estimation of F0 (%)	X	X	X	
tonal	Percentage of tonal time segments		X		
pfmin	Minimum PF			X	
pfmax	Maximum PF		X		
noise	Percentage of noisy time segments			X	

DF: distribution of frequency amplitude; DFB: dominant frequency band; LM: local modulation; PF: peak frequency; F0: fundamental frequency.

Table A3
Description of statistical models

Step of the analysis / model type number	Aim of testing	Replicate	Dependent variable(s)	Fixed factors: qualitative (with levels) and quantitative	Random factors	No. of models run
Preliminary analysis / model type 1	To exclude the possibility that body growth was affected by cross-fostering	Piglet	Body weight	Was the piglet cross-fostered? (Yes-No)	Litter identity	1
Preliminary analysis / model type 2	To exclude the possibility that vocal parameters were systematically changed by cross-fostering	Piglet	40 acoustic variables (10 for each combination of situation and Week, see Table A1)	Was the piglet cross-fostered? (Yes-No)	Litter identity	40 (1 for each variable)
Preliminary analysis / model type 3	To exclude the possibility that weight difference or sex match/mismatch influenced acoustic distance	Piglet dyad	Acoustic distance	Were the two piglets of the same sex? (Yes-No) Weight difference between the two piglets (quantitative)	Litter identity Identity of each of the two piglets	1
Main analysis / model type 4	To assess hypotheses 1, 2 and 3	Piglet * dyad class * age * situation	Mean acoustic distance per piglet and dyad class	Dyad class (Own-Own, Own-OutF, Own-Alien, Own-InF) Age (Week 1, Week 4) Test situation (isolation, back test) Dyad class * age * test situation interactions	Litter identity Piglet identity	1

All models were run as linear mixed models with variance components covariance structure and identity link function. In the preliminary analyses, subsidiary hypotheses were tested that aimed at helping the interpretation of the main analysis results.
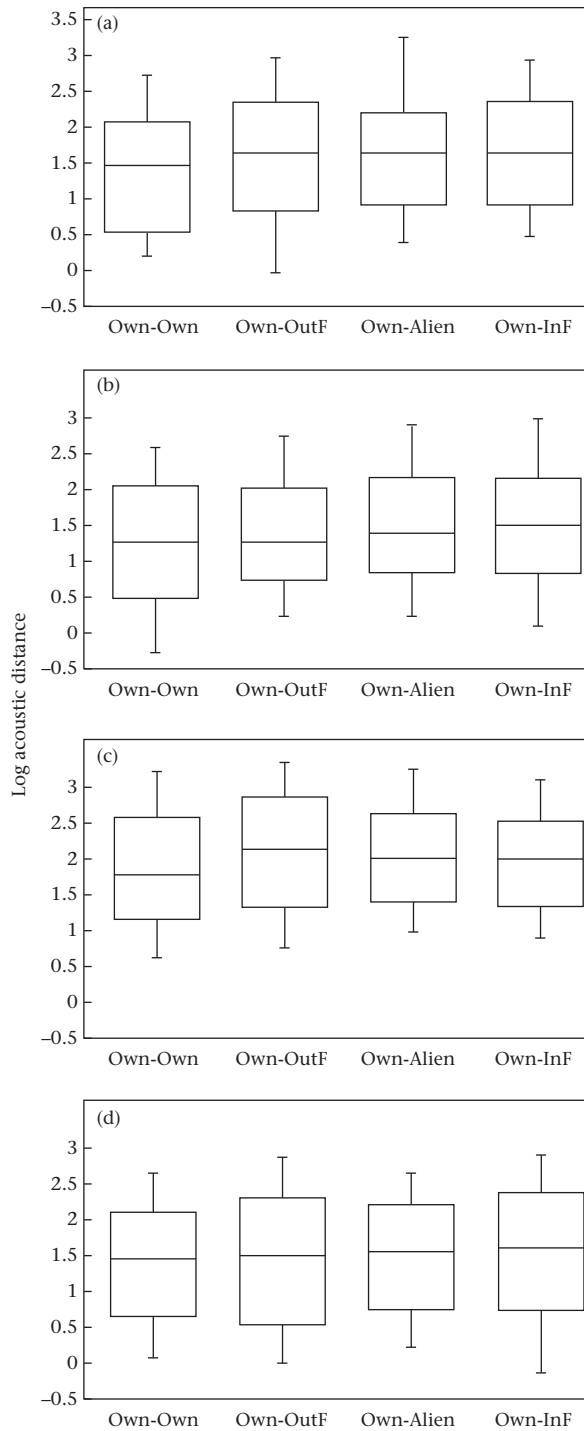
Figure A1. Box plots of the spread of the log-transformed acoustic distances between piglets of different categories. Boxes depict medians with interquartile ranges; whiskers indicate the 0.1 and 0.9 percentiles. (a) Week 1 isolation, (b) Week 1 back test, (c) Week 4 isolation, (d) Week 4 back test. Own = piglets that were born and stayed in the focal litter; OutF = piglets that were born in the focal litter and were fostered neonatally into the other of the two paired litters; Alien = piglets that were born and stayed in the other of the two paired litters; InF = piglets that were born in the other of the two paired litters and were fostered neonatally into the focal litter.