

Cross-species effect of separation calls: family dogs' reactions to pup, baby, kitten and artificial sounds

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During separation, infants of various species often produce a special call type, the separation cry, which elicits instant response from the caregiver. Ignoring this stimulus might be costly; hence, adults have evolved a sensitivity to infant cries. As the acoustic structure and function of these vocalizations are conserved across mammals, adults might react similarly to heterospecific and conspecific separation calls. The domestic dog, *Canis familiaris*, is an excellent model to study reactions to heterospecific vocalizations due to their special niche in the human social environment. Through domestication, they have become especially sensitive to human communicative signals, including baby cries. Furthermore, they can share their natural environment with other species such as other pets and livestock, which could also affect their responsiveness towards heterospecific calls. Taking advantage of this potential cross-species sensitivity, we aimed to examine dogs' reactions to infant separation calls of humans and domestic cats, *Felis catus*, compared to conspecific calls. To explore the effect of novelty and specific acoustic features we also used synthesized cries, which allowed us to look for general rules behind dogs' reactions to heterospecific calls and general acoustic effects functioning across species. After testing 100 dogs with pup cries in a previous study, here we tested another 118 dogs in three groups based on the presented sounds' origin. All stimuli were analysed acoustically; then we tested the effects of the species and acoustic features on the dogs' behaviours. Dogs reacted to pup and artificial cries the fastest, and baby cries the slowest, while responses to kitten sounds were intermediate. We also found general acoustic effects: tonality-related parameters extensively affected the reactions. Higher noisiness caused faster speaker and owner orientation, but it seems that species-specific cues might overwrite the general acoustic rules that appear across mammal separation calls.

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The original definition describes communication as an intra-specific action; however, several examples show that sharing or relying on information from individuals of another species can be adaptive (Goodale, Beauchamp, Magrath, Nieh, & Ruxton, 2010; Westrip & Bell, 2015). In the case of vocal communication, general acoustic rules for encoding emotion are found across species (Andics & Faragó, 2018; Morton, 1977). Hence a certain call type and an innate or learned sensitivity to it in listeners might be the basis of successful cross-species communication. During eavesdropping, an individual other than the 'intended' receiver exploits the signal's

information content. Alarm calls, for example, can elicit antipredator or mobbing behaviours from individuals of other prey species (Magrath, Haff, Fallow, & Radford, 2015). Food calls of others can be exploited too: for example, sika deer, *Cervus nippon*, use the food calls of Japanese macaques, *Macaca fuscata*, to find food sources (Koda, 2012). In both cases interpreting acoustic signals of another species correctly is adaptive allowing individuals to avoid predators and find resources with less investment.

However, sometimes the sensitivity to a given type of signal can be so strong that it elicits a response despite the lack of clear benefit. Specifically, this has been observed in the case of infant distress calls (Lingle & Riede, 2014), which elicit a response from individuals other than the mother. In this case, not reacting to a call that sounds similar and might come from the individual's own

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infant would be costly; thus, 'false positive' reactions are probably not selected against (Bánszegi, Jacinto, Urrutia, Szenczi, & Hudson, 2017). In early life stages of mammals, separation from the mother/caregiver can induce separation calls (a type of distress vocalization), which have highly stereotyped acoustic structure and function (Lingle, Wyman, Kotrba, Teichroeb, & Romanow, 2012; Newman, 2004). The function of this sound type is shared across taxa: attracting the caregivers' attention, reducing the distance between them and inducing parental care (Lingle & Riede, 2014). Reactions can appear as alert behaviour, approaching and retrieving their young, and responding with vocalizations (Bánszegi, Szenczi, Urrutia, & Hudson, 2017; Illmann, Schrader, Špinka, & Šustr, 2002; Lingle & Riede, 2014). The stereotyped structure appears to be due to the similar way in which sounds are produced in most mammals, described by the source–filter theory (Fant, 1960; Titze & Martin, 1998) and Morton's (1977) motivational–structural rules, which state that the similar anatomy and functioning of the vocal apparatus of different species make it possible to produce similar structured sounds in certain situations.

Distress calls are produced in stressful situations and are associated with moderate or high arousal. They can be described as tonal sounds built up from single or repeated short sequences with rich harmonic structure, simple frequency modulations (chevron shape) and in some cases containing nonlinear phenomena (Lingle et al., 2012). Within this structure, several parameters can covary with the arousal level of the individual: high arousal affects parameters that depend on muscle tension (fundamental frequency and amplitude-related parameters) and respiration ratio (calling rate, duration; Briefer, 2012). The communicative function of these key acoustic features can be tested with selected natural calls and synthesized sounds. The latter can elicit a similar response to natural sounds (Aubin, 1989), but can have a less strong effect if their structure is simpler than that of the original signal (Aubin, 1991; Spanier, 1980). Nevertheless, owing to the novelty effect they can also have a stronger effect than natural (known) stimuli.

Interspecific playback studies can provide evidence for the conservative structure and function of certain vocal signals. This stereotyped functioning of distress calls in mammals has been investigated mostly within taxa, for example in Chiroptera (Huang et al., 2018), but there are some studies on unrelated species too (Carrasco & Blumstein, 2012; Kitchen, Bergman, Cheney, Nicholson, & Seyfarth, 2010). In contrast, only one study has investigated the effects of infant separation calls at the interspecific level in wild species: Lingle and Riede (2014) studied the effects of calls of a wider range of species on deer. They found that mule deer, *Odocoileus hemionus*, and white-tailed deer, *Odocoileus virginianus*, mothers responded similarly towards distress calls of various species (marmot, *Marmota flaviventris*, fur seal, *Neophoca cinerea* and *Arctocephalus tropicalis*, bat, *Lasionycteris noctivagans*, human, domestic cat, *Felis catus*, and dog, *Canis familiaris*, etc.) if the range of the fundamental frequency of the calls was similar to that of their own young. In contrast, some playback tests with other call types found that the strength of the reactions to heterospecific vocalizations can decrease with increasing phylogenetic distance (de Kort & ten Cate, 2001; Sosa-López, Martínez Gómez, & Mennill, 2016), and in domesticated animals such as dogs, domestication can also affect sensitivity to heterospecific calls (Andics & Faragó, 2018).

Dogs are good subjects for cross-species communication studies due to their complex social environment (Miklósi & Topál, 2013). They have a long common history with humans (15–32 000 years; Thalmann et al., 2013; Wang et al., 2013) and often share their

environment with other species living close to humans (other pets, livestock, etc.) further enriching the dogs' potential social interactions and experiences. Besides their sensitivity to conspecific distress calls (Lehoczki, Szamosvölgyi, Miklósi, & Faragó, 2019; Quervel-Chaumette, Faerber, Faragó, Marshall-Pescini, & Range, 2016), dogs' special relationship with humans also manifests in their sensitivity to human emotional cues. This has been shown in several studies at the hormonal/physiological (Nagasawa et al., 2015), behavioural (Albuquerque et al., 2016; Huber, Barber, Faragó, Müller, & Huber, 2017; Merola, Prato-Previde, Lazzaroni, & Marshall-Pescini, 2014; Sümegi, Oláh, & Topál, 2014) and neural level (Andics, Gácsi, Faragó, Kis, & Miklósi, 2014). Their reactions to human distress has also been investigated (Custance & Mayer, 2012; Yong & Ruffman, 2014) suggesting a role of emotional contagion in their reactions to human crying; however, no study has compared the reactions of dogs to distress calls of different species.

Our main aim was to test how dogs react to heterospecific separation calls and find out whether individual features and/or species-specific acoustic differences affect their reactions. We used domestic kittens' calls and human baby cries as heterospecific calls and compared these with data on pup calls from our previous study (Lehoczki et al., 2019). To control for novelty, we also played artificial calls. To assess how certain acoustic parameters affect dogs' reactions, we also compared the acoustic structure of the calls from the different species and the artificial calls. Lastly, by testing dogs from different households we were able to investigate whether their experience with human babies affected their reactions during the playback of human baby separation calls.

We formulated the following predictions based on the possible driving forces of the reactions. (1) Conserved acoustic structure effect: we would find no difference in the dogs' attention towards the calls of different species (pup = kitten = human = artificial sounds) due to the stereotypical acoustic structure of separation calls across taxa. (2) Biological voice effect: artificial calls would elicit no or less attention compared to the other two heterospecific playbacks ([pup = kitten = human] > artificial). (3) Phylogenetic distance (acoustic similarity) effect: with increasing phylogenetic distance the level of attention towards the played sound would decrease (pup ≥ artificial > kitten > human). (4) Domestication effect: attention towards the pup and human baby's calls might be similar, owing to the increased sensitivity to human signals in dogs, while attentiveness towards the kitten and artificial calls would be weaker due to having no such relevance ([pup ≥ human] > [kitten = artificial]). (5) Novelty effect: artificial, then kittens' calls would elicit the strongest attention compared to the other two stimuli (artificial ≥ kitten > [human ≥ pup]), as our subjects had no experience with these stimuli.

Additionally, within the human baby calls group, we had the opportunity to directly explore the effect of experience. We supposed that dogs that had experience with children could learn that baby crying is directed towards humans; hence dogs would show more owner-directed behaviours during the playbacks and attend to the stimuli less than dogs with no experience with babies (experienced with babies > inexperienced with babies).

METHODS

Ethical Note

Ethical approval was obtained through the National Animal Experimentation Ethics Committee of Hungary (PEI/001/1056–4/

2015). Owners completed a written consent form, which permitted them to volunteer their dogs to participate in the study.

Subjects

Dog owners were invited from the Family Dog Project's database or recruited by online advertisements on social media. We began by testing 120 dogs in the present study but two subjects had to be excluded because the recording system failed; thus, the final number was 118 (58 males (20 intact, 38 neutered) and 60 females (19 intact, 41 spayed)); age range 1–11 years; mean age \pm SD = 5.13 ± 2.57 years; see [Appendix Table A1](#)). Information about experience with infants of stimuli species (human, cat) was collected from the owners. We also used data of 100 individuals from our previous study on dogs' reactions to pups' separation calls in a similar setting ([Lehoczki et al., 2019](#); 35 males (17 intact, 18 neutered) and 65 females (39 intact, 26 spayed); age range 1–12 years; mean age \pm SD = 3.92 ± 2.43). All dogs were adult, healthy (with no hearing problems based on the owners' report), from various breeds. Purebred and mixed breeds, intact and neutered/spayed dogs both participated in the study. Intact females were tested at least 2 weeks before or after their heat period.

Set-Up and Procedure

Playbacks took place in the laboratory at the Eötvös Loránd University's Ethology Department. The test set-up was identical and the procedure similar to those in our previous study ([Lehoczki et al., 2019](#); see below for differences in playback stimuli).

Test set-up

The test room was divided into two compartments with a removable wooden half-wall including a door. The larger compartment measured 6.27 m x 5.4 m and the smaller 5.2 m x 3 m. Five IP cameras (Basler sca640-120gc) located in the large compartment beyond the ceiling (in the corners and one more in the middle of the removable wall) and one microphone (Sennheiser me-62 with K6 power module; located in the middle, above door A, [Fig. 1](#)) connected to the PC through a Zoom H4n as USB sound card recorded the dog's behaviour (vocal, motor and postural) during the test. The speaker (Genius SP-HF 1800A, 20–20 000 Hz, 50 W, 4 Ohm, 85 dB) was connected to the PC and hidden behind the removable wall between the two compartments. A chair was placed in the middle of the large compartment for the owner to sit on. The video and audio were recorded by a PC system located in a neighbouring room, and the playbacks were controlled on a separate PC with Adobe Audition (Adobe Systems Inc., San Jose, CA, U.S.A.).

Procedure

The owner and dog were led to the test room through door A. Throughout the test the owner sat on the chair, listened to music on headphones and read a book and was also instructed not to interact with the dog to avoid any cuing. The dog was unrestrained and moved freely in the room. In the first minute, after the experimenter left the room through door A, the dog was allowed to explore and habituate to the experimental room. After this silent 1 min warm-up phase, the experimenter started to play the stimuli. For each dog there were four 7 s playbacks of the same type of call

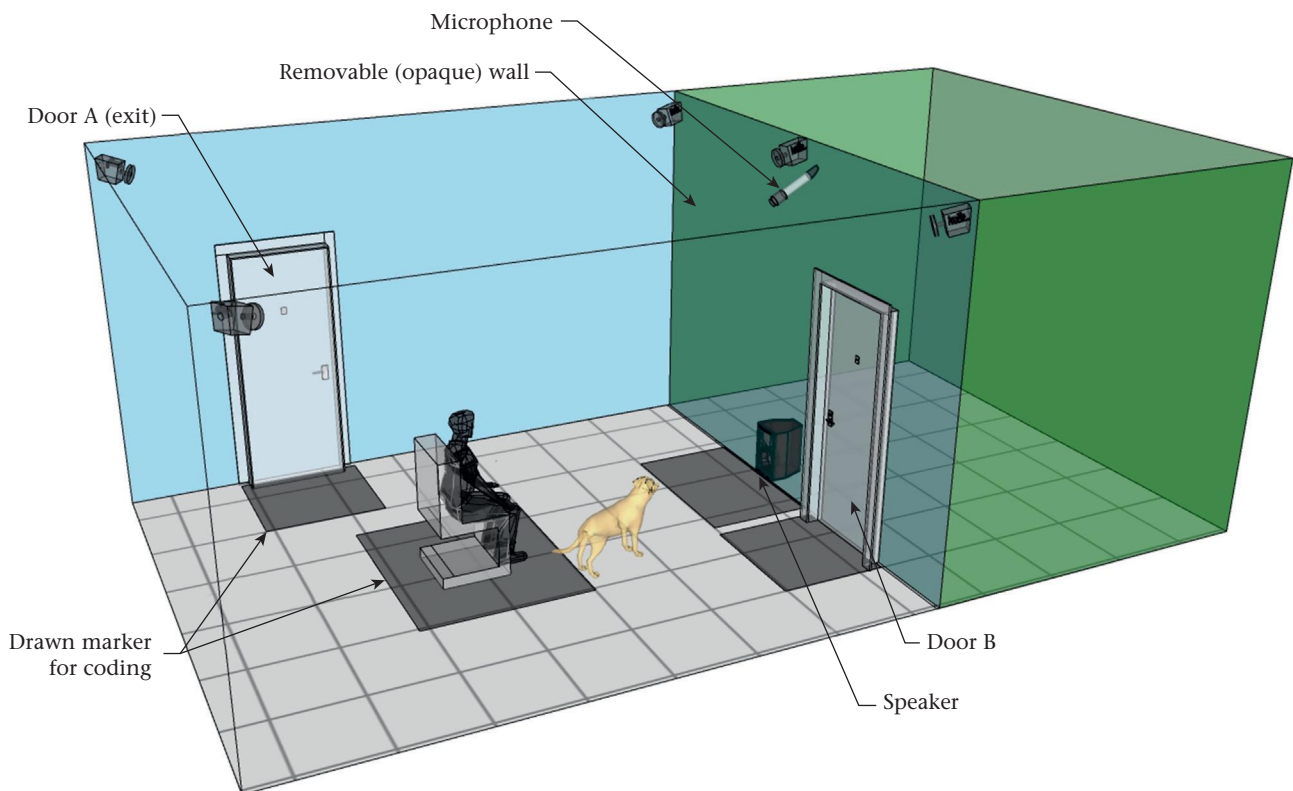
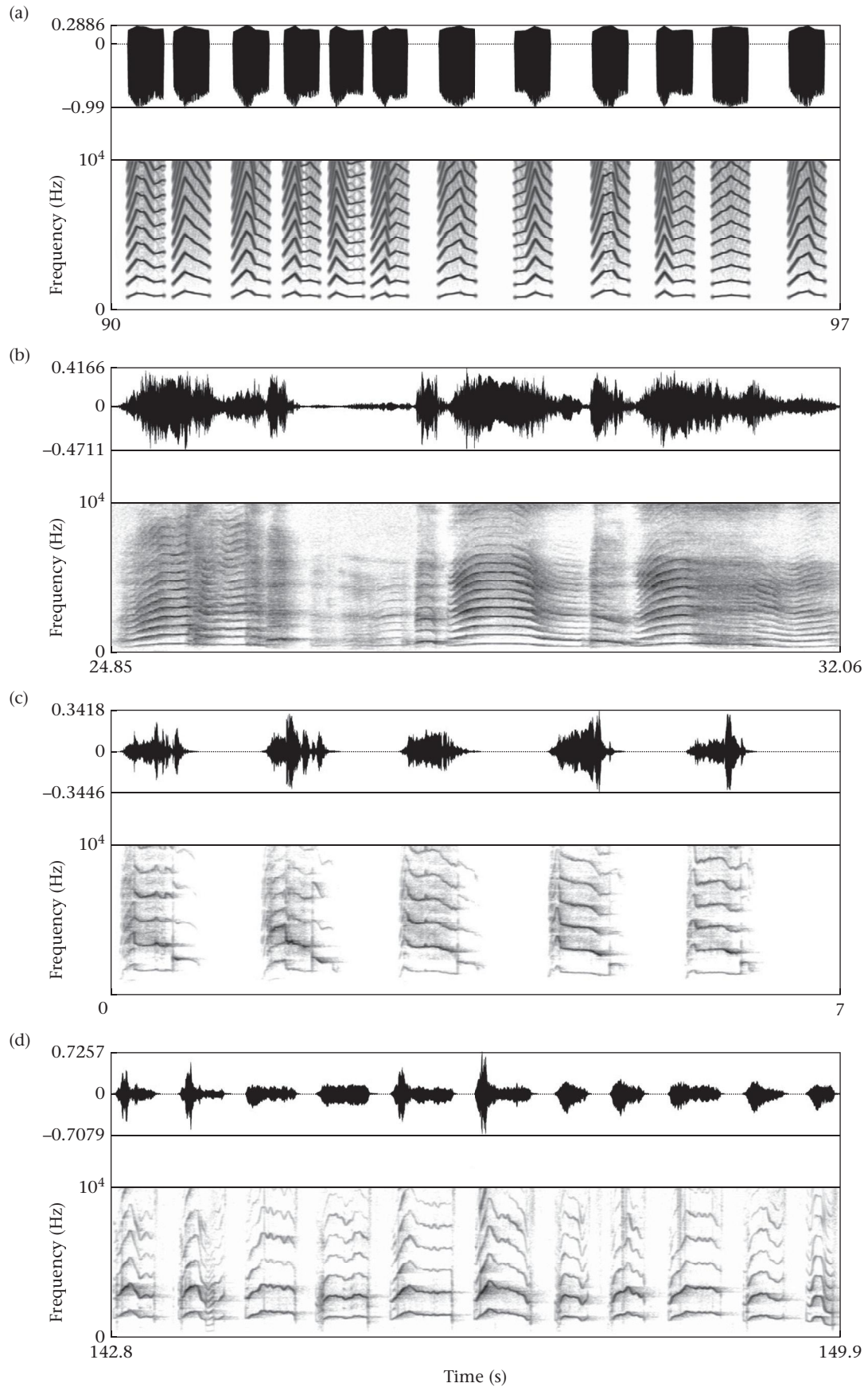


Figure 1. Set-up of the test room. During the test, the owner sat on a chair listening to music and reading a book. The dog moved freely in the room. Four stimuli sounds were played every half minute from the speaker, hidden behind the opaque, removable wall.



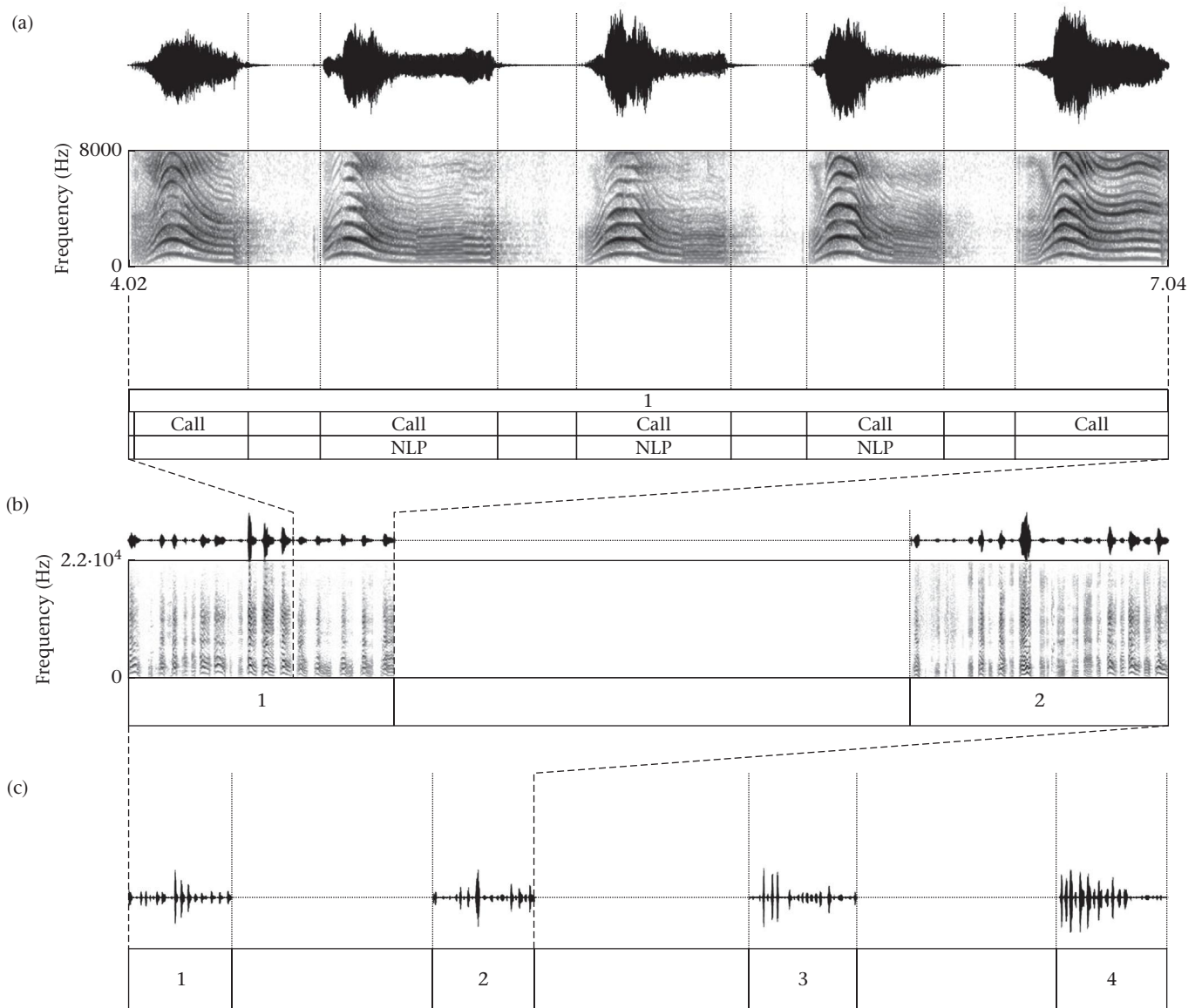


Figure 3. Acoustic analysis of the calls and creation of the stimuli. The figure shows which parts of the pup calls were included in the analysis. (a) During the analysis, after labelling the individual calls, acoustic parameters were defined. Calls and intercall intervals and the detected nonlinear phenomena (NLP) are shown. (b) Playbacks were prepared by cutting the sounds into 7 s long sections. (c) Four sections from the sounds were arranged in a random order to make four playbacks with 30 s silences in between.

separated by silences of 30 s (mean volume was 50 dB with a peak at 60 dB measured from the chair where the owner sat).

Test Sounds

We used three types of stimulus for this playback study, kitten, human baby and an artificial sound, and compared them with our previously obtained data on pup calls (Lehoczki et al., 2019; Fig. 2). We collected separation calls from 13 kittens from four litters from three different mothers on postnatal days 6 and 7 as described in Banszegi, Jacinto, et al. (2017). The calls of the kittens were recorded in a private house. The kittens were removed individually from the nest and transferred to a separate room containing a cardboard recording box (1 x 1 x 1 m) lined with acoustic foam. They almost

immediately produced separation calls. After the first call, we continued recording each kitten for 1 min. Baby separation calls were collected from the database of strange situation tests for babies (SST) conducted by Lakatos et al. (2000). The cries of nine infants (five boys, 12–13 months) were used from their first separation test episode, when the children were left alone in the strange room.

Each recording from kittens and babies was cut into 7 s sections from which we made four stimuli by putting together four sections of a recording from the same individual with intervals of 30 s of silence. Owing to the limited number of baby and kitten sounds, recordings from the same individual were used more than once, but to avoid pseudoreplication we used them in different stimuli and changed the order of the 7 s sections (Fig. 3). In the previous study

Figure 2. Sonogram samples of the (a) artificial sounds, (b) baby cries, (c) kitten calls and (d) pup calls used as playback material. The X axis shows a 7 s bout of each stimulus type, while the Y axis represents the frequency range of the separation calls up to 10 000 Hz. Each subject received four 7 s bouts of the same stimulus type, which were played back from a hidden speaker.

(Lehoczki et al., 2019) we used six 10 s sections of recordings but for the analysis of pup calls in this study we used only the first four of the six sections and only the first 7 s of each section of pup call recordings.

Artificial distress calls were generated by a custom Praat script using the fundamental frequency, call length and jitter values and range of the pup separation calls. From the 64 bouts of calls, each of 7 s, that were generated, we made 16 stimuli by putting together four bouts separated by 30 s of silence.

Dogs were randomly assigned to groups and tested with one of the three stimulus types (Appendix Table A1). Fifty-six dogs were tested with separation calls of human babies. These subjects were further classified into two subgroups depending on their experience with babies. Group 1 consisted of 37 dogs with some experience with babies, having lived with one or more babies under 1 year old ($N = 18$) or having met babies several times ($N = 19$). Group 2 contained 19 dogs that had no experience with babies and had never met a baby less than a year old. We tested 33 dogs with artificial sounds and 29 with kittens' separation calls.

Fifty-five of the dogs had also participated in our previous study (Lehoczki et al., 2019; 25 in the baby call group, 12 in the kitten call group and 17 in the artificial call group). There were at least 6 months between the two studies and statistical analysis showed no effect of retesting on the dogs' behaviour (Appendix Tables A2 and A3). While the dogs in the artificial sound group were certainly naïve about the stimuli, for the kitten call group we had to rely on the owners' opinion about the dogs' experiences. According to the owners, none of our subjects had any experience with kittens; thus, they can be considered naïve about the kitten separation calls too. In our previous study (Lehoczki et al., 2019), dogs with different levels of experience of pup calls were tested. As this had no effect on their reactions, these were pooled for the present analysis.

Acoustic Analysis

All statistical analysis was run in the R environment version 3.6.0 (R Development Core Team, 2019) using R studio (<https://www.rstudio.com>). A semiautomatic custom-made Praat script was used for the acoustic analysis of the separation calls (for details see Lehoczki et al., 2019). From the 40 measured parameters, 21 were selected based on their relevance and used in the analysis (see Appendix Table A4). As a first step the acoustic parameters were scaled to z scores, then principal component analysis (PCA, principal function with oblimin rotation, psych package) was used to reduce the number of dimensions and merge them into components. We used parallel analysis (fa.parallel function, psych package) to determine the optimal number of components. Variables with low loadings were excluded in stepwise manner to find optimal PC structure. Nineteen acoustic parameters (except for f_0 end and call length; the latter was added as a separate variable to the QDA, see below) were combined into five principal components during the PCA (Table 1, Table A5).

Acoustic comparisons

Quadratic discriminant analysis (QDA, qda function, MASS package) was used to check the acoustic discriminability of the four stimulus types based on the PCA scores. Because pup recordings and artificial sequences contained many more calls than recordings of the kittens and babies, we took a random subsample of these stimulus types to obtain a similar number of calls for each type (artificial = 366, baby = 307, kitten = 347, pup = 385). After this we separated the playback stimuli into a training set (60%) and a test set (40%) and ran the QDA on the training set, then tested, with the predict function, the model's discrimination accuracy on the test set. The confusion matrix, overall and within-type accuracy are reported in the Results. Chance level was determined by running the same analysis on five randomized samples of the original acoustic data set. The average accuracy of these control runs was 24%; thus, the chance level was set to this value.

To define which parameters contributed most to the species' differences, we ran generalized linear mixed models (GLMMs, glmer function, lme4 package) with Tukey post hoc pairwise comparisons (emmeans and cld function, emmeans package) on all the calls used in the playbacks. The PC scores (see Results) were Box–Cox transformed if they differed from a normal distribution or an appropriate link function was applied. Models included species as the main effect and subject ID as a random factor.

Video and Data Analysis

We analysed the dogs' behaviour during playbacks from the videos, using Solomon coder (Péter, 2014) with a 0.2 s time resolution. Coded behaviour variables and measurements (percentage or latency) are shown in Appendix Table A6. The coding reliability was determined using kappa statistics based on 20% of the sample recoded by an independent coder blind to the purpose of the tests. Average kappa was 0.834 ± 0.227 . All statistical analysis was run in the R environment version 3.6.0 (R Development Core Team, 2019) using R studio (RStudio Team, 2012).

To be able to compare the behaviour of the dogs we applied the same PCA structure that was used in our previous study (Lehoczki et al., 2019; see Results). Seventeen percentage variables (three of the 20 behaviour variables were excluded) were combined into six principal components (Table 2, Table A7). PC scores for the current data were calculated using the predict.principal function of the psych package.

We used GLMMs (nlme package, lme function, controlling for heteroscedasticity) for analysing PCs, which were used as a separate response variable. Parsimonious models were identified with stepwise backwards elimination-based model selection (MASS and lme4 packages, drop1 function). The PC scores were Box–Cox transformed if they differed from a normal distribution.

For the latencies, mixed-effect Cox regression was applied (coxme package). Subject ID was included as a random factor in both Cox and GLMM models. Initial models included species,

Table 1
Distribution of the measured acoustic parameters between the five components formed by PCA

Pitch range	Dominant pitch	Pitch contour	Spectral form	Tonality
Fundamental frequency range	Average height of frequencies in a spectrum	Position of minimum fundamental frequency	Skewness	Mean tonality
Standard deviation of the fundamental frequency	Non-normalized skewness of the spectrum	Position of maximum fundamental frequency	Kurtosis	Standard deviation of tonality
Maximum fundamental frequency	Minimum fundamental frequency	Fundamental frequency change		Maximum tonality
Mean fundamental frequency				Jitter
				Entropy

Table 2
Distribution of the coded behaviour variables between the six components formed by PCA

Attention	Stand	Owner	Speaker	Stress	Door
Orient to speaker	Lie	Orient to owner	Proximity to speaker	Whine	Orient to door
Listening	Stand	Touch owner	Explore speaker	Proximity to exit	Proximity to door
Move		Bark		Proximity to owner	
Explore lab		Woof			

playback number (1–4), sex and reproductive status as fixed factors. Besides these, acoustic PCA components and dog age were included as covariates, respectively. In addition, interactions were included between sex and reproductive status and also between playback number and all the other factors and covariates to check for habituation effects. As in our previous study (Lehoczki et al., 2019), individual features of the dogs such as sex and reproductive status had no effect on their behaviour and were not included in the final models.

RESULTS

Acoustic Comparisons

Based on the PCA scores the QDA showed a high 84% accuracy, suggesting a good discriminability between the four stimulus types. The confusion matrix (Table 3) suggests that the baby separation calls were acoustically somewhat closer to the calls of the pups than to the other two types of calls. Calls of the kittens were confused by the QDA only with the calls of the pups, while pup calls seemed to be more similar to baby cries than to the kitten calls. Artificial calls were the most distinct type in our stimuli set.

According to the GLMMs the species' calls differed in all acoustic principal components. Dominant pitch was highest in artificial sounds and lowest in the calls of babies and pups (these did not differ significantly) while the kittens' calls were intermediate ($\chi^2_3 = 178.94$, $P < 0.001$; Fig. 4a). As call length did not fit into any components, we tested it separately, but found no difference suggesting that all calls fell into the same length range ($\chi^2_3 = 6.127$, $P = 0.106$; Fig. 4b). The pitch contour of artificial calls had a more rising pattern than babies' and pups' calls ($\chi^2_3 = 13.85$, $P = 0.003$; Fig. 4c). Spectral form, which includes skewness and kurtosis, was significantly higher in the calls of pups and kittens than in babies and artificial sounds ($\chi^2_3 = 24.84$, $P < 0.001$; Fig. 4d). Pitch range was highest in kittens while the calls of babies had significantly lower scores than the calls of pups ($\chi^2_3 = 41.844$, $P < 0.001$; Fig. 4e). Finally, kittens' calls and artificial sounds were more tonal than babies' and pups' calls ($\chi^2_3 = 30.52$, $P < 0.001$; Fig. 4f).

Behaviour

Stimulus type effects

The latency to orient to the speaker was affected by the type of stimulus: dogs reacted significantly faster to the artificial sounds than to babies' calls ($\text{exp}\beta$ (95% confidence interval, CI)=1.879

(1.201–2.940), $z = 3.28$, $P = 0.006$). Calls of babies also tended to elicit a slower reaction than the calls of pups ($\text{exp}\beta$ (95%CI)=0.699 (0.484–1.011), $z = -2.52$, $P = 0.057$; Fig. 5) while kitten calls were intermediate and not significantly different from baby and pup calls. Time spent next to the speaker was also affected by stimulus type (likelihood ratio test, LRT: $\chi^2_3 = 7.894$, $P = 0.048$): dogs spent least time next to the speaker when they heard the calls of babies and most when they heard the calls of pups ($\beta \pm \text{SE} = 0.026 \pm 0.009$, $t_{213} = 2.751$, $P = 0.033$) while the other two types of calls were intermediate.

Acoustic effects

For both latency to orient to the speaker and latency to orient to the owner, we found a significant negative effect of tonality: noisier calls caused faster orientation to the speaker ($\text{exp}\beta$ (95%CI)=0.832 (0.721–0.973), $z = -2.3$, $P = 0.022$) and to the owner ($\text{exp}\beta$ (95%CI)=0.819 (0.679–0.989), $z = -2.08$, $P = 0.038$; Fig. 6). Latency to orient to the owner was also affected by average call length: the longer the calls were in the bout, the shorter the contact was with the owner ($\beta \pm \text{SD} = 0.042 \pm 0.014$, $t_{647} = 2.887$, $P = 0.004$). For behaviours related to stress (whining and proximity to exit and owner), we found a significant interaction between playback number and the pitch contour (LRT: $\chi^2_3 = 13.404$, $P = 0.004$; Fig. 7). A rising pitch contour was associated with more stress-related behaviours in the first two playbacks, but this effect disappeared in the last two (for post hoc test results see Table A8). There were no significant acoustic effects for other behaviours associated with the speaker or door.

Habituation effect

A general habituation effect was found for the latency to orient to the speaker (Cox regression, LRT: $\chi^2_3 = 33.59$, $P < 0.001$; Table A9) and attention (orienting to the speaker, listening, moving and exploring the laboratory; LRT: $\chi^2_3 = 40.647$, $P < 0.001$; Table A10) and a nonsignificant trend for proximity to and exploring the speaker (LRT: $\chi^2_3 = 7.426$, $P = 0.059$). Scores for behaviours related to the owner, however, increased from the first to the fourth playback (LRT: $\chi^2_3 = 16.659$, $P = 0.001$; Table A11).

Age-related effects

We found a negative effect of age for latency to orient to the speaker ($\text{exp}\beta$ (95%CI)=0.954 (0.914–0.995), $z = -2.17$, $P = 0.03$), showing that younger dogs looked towards the speaker faster during the playback. Younger dogs also showed more stress-related

Table 3
Confusion matrix based on the four stimuli types' PCA scores

Predicted stimulus type	Actual sample	Actual sample			
		Artificial	Baby	Kitten	Pup
Artificial	145	1	0	1	
Baby	0	77	0	8	
Kitten	0	0	126	13	
Pup	1	45	13	132	

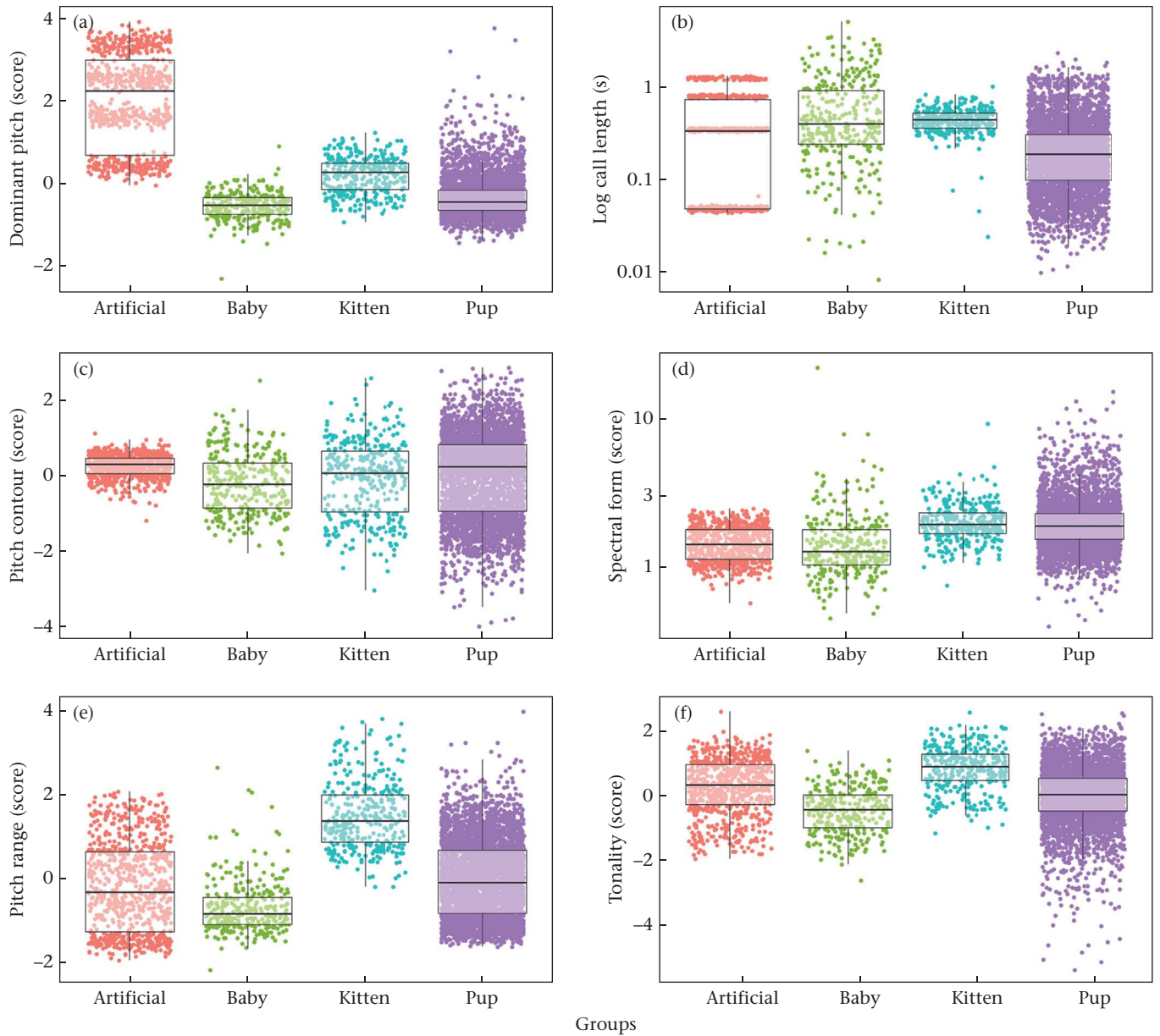


Figure 4. Acoustic differences between the four stimuli types (artificial, baby, kitten, pup). Scores of the acoustic PCA components: (a) dominant pitch; (c) pitch contour; (d) spectral form; (e) pitch range; (f) tonality. (b) Call length (s). Each dot represents one call in the analysis. Box plots show the medians (horizontal lines), upper and lower quartiles (boxes) and lowest and highest values within 1.5 times the interquartile range (whiskers).

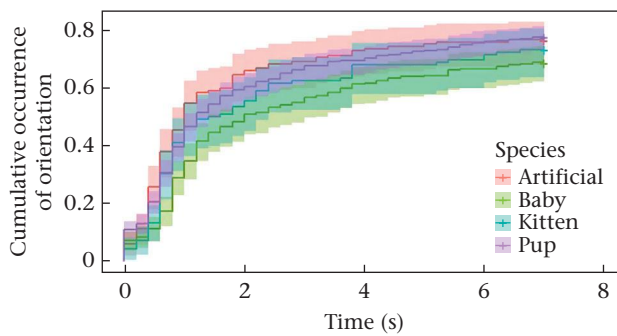


Figure 5. Changes in the latency to orient to the speaker measured from the start of the playback in relation to stimulus type. The lines show the likelihood of orientation occurring at a given time point and the shading shows the 95% confidence intervals for the median.

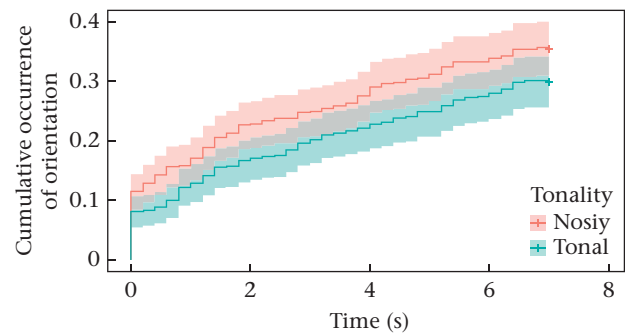


Figure 6. Changes in the latency to orient to the owner over time in relation to tonality. The tonal–noisy cutoff was made at the median of the continuous variable for visualization only. The lines show the likelihood of orientation occurring at a given time point and the shading shows the 95% confidence intervals for the median.

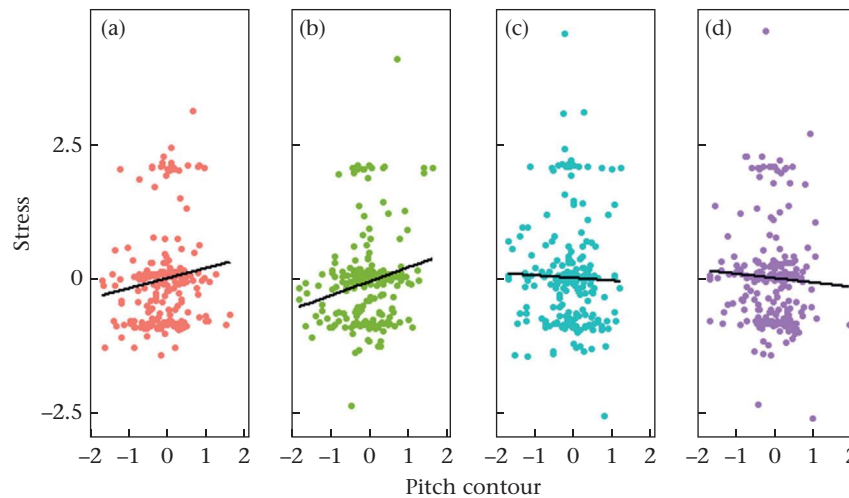


Figure 7. Effect of pitch contour on stress-related behaviours over the four playbacks in each test. (a) Playback 1, (b) playback 2, (c) playback 3 and (d) playback 4. Both variables are PCA components; thus, the axes show scores. Dots represent the individuals' stress PCA score related to one 7 s playback, while the trendline shows the direction and strength of the effect.

($\beta \pm \text{SD} = -0.017 \pm 0.005$, $t_{211} = -3.398$, $P = 0.001$) and owner-related behaviours ($\beta \pm \text{SD} = -0.005 \pm 0.003$, $t_{212} = -1.969$, $P = 0.05$).

Baby calls playback groups

We found a significant interaction effect between experience and playback number (LRT: $\chi^2_3 = 8.740$, $P = 0.033$; Fig. 8). The post hoc analysis also showed a difference in habituation between the two groups: dogs that had no experience with babies did not habituate to the cries, whereas in dogs that had experience there was a significant drop in attention across the four playbacks (Table A12).

DISCUSSION

The aim of this study was to test how dogs react to hetero-specific separation calls and what individual and acoustic factors affect their reactions. We found general acoustic effects independent of type of stimulus, suggesting they depend on the conserved acoustic structure of distress calls, but species-specific cues affected the dogs' sensitivity more, indicating an effect of phylogenetic distance between the callers. The attention of dogs decreased with increasing phylogenetic distance: they reacted slower to human baby cries than pup calls, while kitten calls elicited an intermediate reaction. This somewhat contradicts the findings of Lingle and Riede (2014) as they reported a similarly strong reaction (approach) in deer independent of the source species. Dogs' ancestors originally had den-dwelling litters with little chance of pups getting lost, leading to lower selection pressure on canids to avoid false positive reactions (see also Bánszegi, Szenczi, et al., 2017) in contrast to deer species that hide their offspring (Peterson & Geist, 2000). This could result in dogs reacting less to heterospecific than conspecific calls. Modern dogs living in the human environment probably face even less risk of not reacting appropriately to distress calls. However, Lingle and Riede (2014) also found that if the hetero-specific calls' fundamental frequency fell into the natural range of the deer calls the mothers' reaction was stronger supporting our findings on the importance of species-specific cues.

Although the general structure of distress calls is similar across species (Lingle et al., 2012), because the neural control of voice production is not fully developed in young individuals we can expect a high within-individual variability in all species' separation calls, which might occlude the species-specific differences.

However, using QDA and GLMMs we found acoustic differences between the separation calls of kittens, pups and human infants. Among these, calls of the kittens had the highest scores on the dominant pitch, pitch range, spectral form and tonality components. These differences could be the result of evolutionary differences between the species' vocal repertoires that probably already affect their calls at this young age or of anatomical and morphological differences. We found that of the three species, pup and baby cries were more like each other, while kitten cries were further from baby cries than from pup cries acoustically. This somewhat contradicts what one would expect based on phylogenetic relations between the species. Body size might be a reason behind the fundamental frequency-related differences between baby cries and kitten calls (i.e. dominant pitch, pitch range and pitch contour) as these parameters depend on the larynx and vocal fold size (Titze, Riede, & Mau, 2016) and on the scaling of body size (Bowling et al., 2017) and weight (Charlton & Reby, 2016) between species. Kittens having the smallest body size and babies the largest are in line with this, but the acoustic similarity of pup and baby cries contradicts this and is surprising. Within species, pup calls covered the widest range in pitch contour and tonality, overlapping with the other species' calls. This high variability might be the reason behind this finding, which could be due to the lack of selection pressure on dogs to have a more species-specific call structure. As Taylor and Reby (2010) suggested in their study on the source-filter theory, the size of the vocal tract can also depend on body size, which can modify the acoustic parameters of the sound wave produced in the larynx across different formants (spectral peaks). However, differences in morphology of the supralaryngeal tract with all its air cavities can cause differences between species' call acoustics (Gamba, Friard, & Giacoma, 2012).

Tonality parameters and spectral form can both be related to the level of development of neural control of the voice and the affective state of the individual (Jürgens, 2009). Imprecise control of voice production can lead to high variation in the vocal fold vibrations, instability of the vocal cycles and the high occurrence of nonlinear phenomena (Kent & Murray, 1982; Mende, Herzel, & Wermke, 1990). Kittens develop faster than pups (e.g. development of the nervous system in kittens is ca. 1 week faster than it is in dogs, Fox, Inman, & Himwich, 1967; Lavelly, 2006; Villablanca & Olmstead, 1979) which can affect vocalizations produced by the laryngeal muscle (Ehret, 1980). In line with this, one would expect that, as the

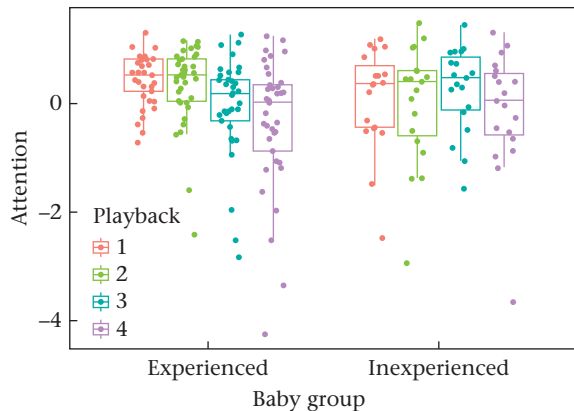


Figure 8. Duration of the PCA component attention towards baby cries over the four playbacks in a test. Experienced: dogs that had either lived with babies under 1 year of age or had met babies several times. Inexperienced: dogs that had never met babies younger than 1 year. Each point represents the data of an individual dog. Box plots show the medians (horizontal lines), upper and lower quartiles (boxes) and lowest and highest values within 1.5 times the interquartile range (whiskers).

babies in our sample were around 1 year old, they would have the most tonal cries; however, we found the opposite, baby cries were the harshest. Human infants at this age are highly dependent on their caretakers and are already showing attachment to their mother (Ainsworth & Bell, 1970). They may also have more advanced cognitive abilities than pups and kittens at the age we recorded their cries (4 days). Thus the experience and perception of separation from the mother could be much more stressful and lead to the babies' affective state being different from those of the other two species. Higher harshness in the babies' cries could thus indicate their higher arousal level (Briefer, 2012; Fitch, Neubauer, & Herzel, 2002; Lenti Boero, Bianchi, Volpe, Marcello, & Lenti, 1998; Lingle et al., 2012). It is also possible that 1-year-old babies have already developed volitional control of their vocalizations and may be able to manipulate their voice to sound harsher and more stressful to regain contact with their mother during separation.

Results of the QDA suggest that the artificial cries we generated were distinct from the other calls. This may be because, although the parameters used for their production were defined on the basis of separation calls of pups, their structure was kept simple (only the fundamental frequency, call length and jitter were defined).

The species effects we found are not in line with the acoustic differences between the calls. It seems that the basic acoustic parameters conserved across species affected how the dogs reacted to the separation calls. We found that, regardless of species, tonality affected the dogs' behaviour: noisy sounds, which may be related to a more aroused, negative affective state, resulted in faster orientation to the speaker and owner. While the former could be due to the attention-attracting effect of harshness (see nonlinearity hypothesis, Fitch et al., 2002), simple emotional contagion may explain the effect on owner orientation (Briefer, 2018; Huber et al., 2017; Quervel-Chaumette et al., 2016). Dogs may initially turn towards their owners before comfort seeking or alternatively they may be social referencing as already shown in dogs facing a novel, scary object (Merola, Prato-previde, & Marshall-Pescini, 2012).

We also found that a rising pitch contour in the calls was associated with more stress-related behaviours, although this effect was present only in the first two playbacks. Interestingly, in her review Briefer (2012) did not find any associations between emotions and different pitch contours reported in the literature. However, McComb, Taylor, Wilson, and Charlton (2009) found that humans perceived cat purrs as more urgent and less pleasant when

they contained a peak in pitch; these sounds were recorded in a food-soliciting context. A rising pattern in fundamental frequency (at least in speech) might function to attract attention and elicit a response (Papoušek, Papoušek, & Symmes, 1991) and thus might have elicited a stronger initial stress response from the dogs. Based on the pattern of responses over the four playbacks, it seems that this change in association between pitch contour and stress-related behaviours was not due to habituation; rather, in the later playbacks, calls with a lower pitch contour elicited stronger stress-related behaviours suggesting the calls had an overall sensitizing effect. These overarching acoustic effects suggest key features of separation calls function the same way across species. The fact that the artificial calls, although distinct from the biological sounds, elicited similar responses to the pup calls shows that neither the novelty nor their artificial nature had a notable effect on the dogs, further supporting the importance of these key features.

We found no effect of the dogs' sex on their reaction to hetero-specific separation cries, which is in line with the results found in our previous study with only pup separation calls (Lehoczki et al., 2019). This may be related to relaxed selection pressure on modern dogs' parental behaviour in the human environment which could blur potential sex differences in responsiveness. However, our results showed that younger dogs reacted more, were more stressed and tried to interact with the owner more. This shows similarities with the results of Kubinyi, Turcsán, and Miklósi (2009), who found that young dogs were less calm, in general, than older dogs based on questionnaire results, while old dogs in a recent study were found to be less excitable (Wallis, Szabó, & Kubinyi, 2020). Based on these studies, it is possible that the higher reactivity of young dogs is related not specifically to call type but to their higher general energy level (activity) than older ones.

Finally, in the 'baby group' analysis, in contrast to our hypothesis, we found no higher-level owner-oriented behaviour and less attention in experienced dogs. While dogs with experience of baby cries showed clear habituation across the four playbacks, dogs with no such experience did not habituate. Yong and Ruffman (2014) found that dogs from child-free households showed similar reactions to dogs experienced with babies, but habituation was not compared between the two groups. We suggest that sensitivity to this call type in experienced dogs decreases because of learning, whereas for inexperienced dogs, this sound is a strong unknown stimulus.

Conclusions

Although dogs undoubtedly have a special relationship with humans, and they show a preference for humans from an early age, it seems domestication has not changed their reaction to infant separation calls. Besides the general acoustic effects of specific key features (such as tonality), their reactions were still mostly affected by the stimulus type. This could be caused by a phylogenetic effect; however, it could also simply be related to the morphological differences between the species. Further studies with more species included could help clarify these issues.

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Appendix

Table A1
Subjects of the study

ID	Sex	Sexual state	Age (years)	Breed	Sound	Baby experience
1	Male	Intact	7.5	Cocker spaniel	Artificial	–
2	Female	Neutered	10	Labrador retriever	Artificial	–
3	Male	Neutered	1.5	Mix	Artificial	–
4	Male	Neutered	3	Pekingese	Artificial	–
5	Female	Neutered	4	Hungarian vizsla	Artificial	–
6	Male	Neutered	7	Mix	Artificial	–
7	Female	Neutered	7.5	Mix	Artificial	–
8	Female	Neutered	2.5	Mix	Artificial	–
9	Female	Neutered	4	Mix	Artificial	–
10	Female	Neutered	5	Mix	Artificial	–
11	Female	Intact	6	Dachshund	Artificial	–
12	Female	Neutered	5	Mix	Artificial	–
13	Male	Neutered	3.5	Mix	Artificial	–
14	Male	Neutered	4	Parson Russell terrier	Artificial	–
15	Male	Neutered	3	Hungarian vizsla	Artificial	–
16	Male	Neutered	3	Mix	Artificial	–
17	Female	Neutered	2	Siberian husky	Artificial	–
18	Male	Intact	8.5	Hovawart	Artificial	–
19	Female	Neutered	4.5	Puli	Artificial	–
20	Female	Neutered	10	Dachshund	Artificial	–
21	Female	Intact	4	Mix	Artificial	–
22	Female	Intact	2	Dachshund	Artificial	–
23	Male	Neutered	3	Dachshund	Artificial	–
24	Female	Intact	2	Border collie	Artificial	–
25	Female	Intact	9	Border collie	Artificial	–
26	Female	Intact	6	Border collie	Artificial	–
27	Male	Neutered	8	Boxer	Artificial	–
28	Female	Intact	6.5	Border collie	Artificial	–
29	Female	Neutered	3	Mix	Artificial	–
30	Male	Neutered	5	Mix	Artificial	–
31	Female	Intact	2	Munsterlander	Artificial	–
32	Female	Intact	2.5	Labrador retriever	Artificial	–
33	Female	Neutered	3	Hungarian vizsla	Artificial	–
34	Male	Neutered	4.5	Mix	Baby	Experienced
35	Female	Neutered	2	Labrador retriever	Baby	Inexperienced
36	Female	Neutered	7.5	Mix	Baby	Experienced
37	Female	Neutered	3	Mix	Baby	Experienced
38	Male	Neutered	2.5	Mix	Baby	Experienced
39	Male	Neutered	4.5	Mix	Baby	Experienced
40	Male	Intact	8	Golden retriever	Baby	Experienced
41	Female	Neutered	7.5	Yorkshire terrier	Baby	Inexperienced
42	Male	Intact	4	Hungarian vizsla	Baby	Experienced
43	Female	Neutered	7	Mix	Baby	Inexperienced
44	Male	Neutered	4	German shepherd	Baby	Inexperienced
45	Male	Neutered	5.5	Mix	Baby	Inexperienced
46	Female	Neutered	8.5	Schipperke	Baby	Inexperienced
47	Female	Neutered	10	Mix	Baby	Experienced
48	Female	Neutered	7.5	American Staffordshire terrier	Baby	Experienced
49	Male	Intact	3.5	Golden retriever	Baby	Inexperienced
50	Female	Neutered	8.5	Mix	Baby	Inexperienced
51	Male	Intact	4.5	Labrador	Baby	Experienced
52	Male	Intact	1.5	Border collie	Baby	Inexperienced
53	Female	Neutered	6	Labrador	Baby	Experienced

Table A1 (continued)

ID	Sex	Sexual state	Age (years)	Breed	Sound	Baby experience
54	Male	Intact	4.5	Mudi	Baby	Experienced
55	Female	Neutered	2.5	Irish setter	Baby	Inexperienced
56	Male	Neutered	1.5	Mix	Baby	Inexperienced
57	Male	Neutered	3	Mix	Baby	Experienced
58	Female	Neutered	11	Mix	Baby	Experienced
59	Male	Neutered	1.5	Mix	Baby	Experienced
60	Male	Neutered	4	Mix	Baby	Inexperienced
61	Male	Intact	4.5	English cocker spaniel	Baby	Experienced
62	Male	Intact	6	Fox terrier	Baby	Inexperienced
63	Male	Neutered	4.5	Mix	Baby	Experienced
64	Female	Neutered	4.5	Hungarian vizsla	Baby	Experienced
65	Female	Neutered	2	Dachshund	Baby	Experienced
66	Female	Intact	3	Border collie	Baby	Experienced
67	Male	Neutered	7.5	Border collie	Baby	Inexperienced
68	Female	Neutered	6.5	Beagle	Baby	Experienced
69	Male	Neutered	6	Yorkshire terrier	Baby	Experienced
70	Male	Neutered	1.5	Pug	Baby	Experienced
71	Male	Neutered	3	Mix	Baby	Inexperienced
72	Male	Intact	4	Pyrenean mountain dog	Baby	Experienced
73	Male	Neutered	9	English cocker spaniel	Baby	Experienced
74	Male	Intact	4.5	Shar Pei	Baby	Experienced
75	Female	Neutered	5	Mix	Baby	Experienced
76	Female	Neutered	9.5	Labrador retriever	Baby	Experienced
77	Male	Neutered	6	Mix	Baby	Experienced
78	Female	Neutered	10	Yorkshire terrier	Baby	Experienced
79	Female	Intact	6.5	Hovawart	Baby	Experienced
80	Male	Intact	2	Kangal	Baby	Inexperienced
81	Female	Neutered	2.5	Saluki	Baby	Experienced
82	Male	Neutered	4.5	Dachshund	Baby	Experienced
83	Female	Neutered	4.5	Miniature schnauzer	Baby	Experienced
84	Female	Neutered	8	Mix	Baby	Inexperienced
85	Male	Intact	6	Malinois	Baby	Experienced
86	Male	Neutered	10.5	Schipperke	Baby	Inexperienced
87	Female	Neutered	5	Border collie	Baby	Experienced
88	Female	Neutered	4.5	Mix	Baby	Experienced
89	Female	Neutered	6.5	Golden retriever	Baby	Inexperienced
90	Female	Neutered	8	Transylvanian hound	Kitten	–
91	Male	Intact	7	Labrador retriever	Kitten	–
92	Male	Neutered	4	Mix	Kitten	–
93	Male	Neutered	2.5	Mix	Kitten	–
94	Female	Intact	3.5	Transylvanian hound	Kitten	–
95	Female	Neutered	2	Hungarian vizsla	Kitten	–
96	Female	Intact	1	Beagle	Kitten	–
97	Male	Intact	6.5	Border collie	Kitten	–
98	Male	Neutered	7	Mix	Kitten	–
99	Male	Intact	5	Dachshund	Kitten	–
100	Male	Intact	9	Yorkshire terrier	Kitten	–
101	Male	Intact	9	Havanese	Kitten	–
102	Female	Intact	9	Bolognese	Kitten	–
103	Male	Intact	2	Swiss white shepherd	Kitten	–
104	Female	Intact	7.5	Pointer	Kitten	–
105	Male	Intact	2.5	Shiba inu	Kitten	–
106	Female	Intact	2	Papillon	Kitten	–
107	Male	Neutered	4	Mix	Kitten	–
108	Male	Neutered	4	Mix	Kitten	–
109	Female	Neutered	4.5	Puli	Kitten	–
110	Female	Neutered	6	Border collie	Kitten	–
111	Male	Neutered	3	Hungarian vizsla	Kitten	–
112	Male	Neutered	5	Hungarian greyhound	Kitten	–
113	Female	Intact	6	Mudi	Kitten	–
114	Female	Neutered	3	Mix	Kitten	–
115	Male	Neutered	3	Weimaraner	Kitten	–
116	Male	Neutered	11	Weimaraner	Kitten	–
117	Male	Neutered	11	Golden retriever	Kitten	–
118	Female	Intact	5	Airedale terrier	Kitten	–
119	Male	Intact	3	Belgian shepherd	Pup	–
120	Female	Intact	8	Hovawart	Pup	–
121	Female	Intact	7	Coton de Tulear	Pup	–
122	Female	Intact	7	Coton de Tulear	Pup	–
123	Male	Intact	3	Mix	Pup	–
124	Male	Neutered	6	Beauceron	Pup	–
125	Male	Intact	5	Malinois	Pup	–
126	Female	Neutered	6	Beagle	Pup	–
127	Male	Intact	1	Mix	Pup	–

(continued on next page)

Table A1 (continued)

ID	Sex	Sexual state	Age (years)	Breed	Sound	Baby experience
128	Male	Neutered	2	Mix	Pup	—
129	Female	Intact	3	Cavalier King Charles spaniel	Pup	—
130	Male	Neutered	12	Mix	Pup	—
131	Female	Intact	1.5	Standard schnauzer	Pup	—
132	Female	Intact	2.5	Newfoundland	Pup	—
133	Female	Neutered	6	Mix	Pup	—
134	Female	Neutered	3	Fox terrier	Pup	—
135	Male	Neutered	4.5	Mix	Pup	—
136	Female	Intact	4	Border collie	Pup	—
137	Male	Intact	5	Mix	Pup	—
138	Male	Neutered	2	Siberian husky	Pup	—
139	Female	Intact	2	Chihuahua	Pup	—
140	Female	Neutered	4.5	Mix	Pup	—
141	Male	Intact	3.5	German shepherd	Pup	—
142	Male	Neutered	5	Mix	Pup	—
143	Female	Intact	8	Collie	Pup	—
144	Female	Neutered	8	Mix	Pup	—
145	Male	Intact	3	Dachshund	Pup	—
146	Female	Neutered	8	Mix	Pup	—
147	Female	Intact	2.5	Collie	Pup	—
148	Female	Intact	5	Yorkshire terrier	Pup	—
149	Female	Intact	6	Airedale terrier	Pup	—
150	Male	Neutered	7	Mix	Pup	—
151	Female	Neutered	2.5	Basset hound	Pup	—
152	Male	Neutered	4	Mix	Pup	—
153	Male	Intact	1	Beauceron	Pup	—
154	Female	Intact	1	Mix	Pup	—
155	Male	Intact	3	Siberian husky	Pup	—
156	Female	Intact	6.5	Great dane	Pup	—
157	Male	Neutered	6	Hungarian vizsla	Pup	—
158	Female	Intact	2	Mudi	Pup	—
159	Female	Intact	2.5	Dachshund	Pup	—
160	Male	Neutered	5	Mix	Pup	—
161	Male	Intact	6	Fox terrier	Pup	—
162	Female	Intact	2.5	Border collie	Pup	—
163	Male	Intact	2	Siberian husky	Pup	—
164	Female	Intact	1.5	Border collie	Pup	—
165	Male	Intact	5	Boxer	Pup	—
166	Female	Neutered	4	Mix	Pup	—
167	Female	Intact	6	Papillon	Pup	—
168	Female	Neutered	1.5	Mix	Pup	—
169	Female	Intact	1	Mix	Pup	—
170	Female	Neutered	2	Mix	Pup	—
171	Female	Neutered	1	Mix	Pup	—
172	Female	Neutered	1	Hungarian vizsla	Pup	—
173	Female	Intact	1.5	Golden retriever	Pup	—
174	Female	Intact	1	Moscow watchdog	Pup	—
175	Female	Intact	4.5	Mix	Pup	—
176	Female	Neutered	4	Mix	Pup	—
177	Female	Intact	1	Siberian husky	Pup	—
178	Male	Neutered	7	Mix	Pup	—
179	Male	Neutered	5	Mix	Pup	—
180	Female	Intact	3	Border collie	Pup	—
181	Female	Intact	2	Cavalier King Charles spaniel	Pup	—
182	Female	Neutered	1.5	Mix	Pup	—
183	Female	Neutered	7	Border collie	Pup	—
184	Male	Intact	4	Aussie	Pup	—
185	Female	Neutered	7	Hovawart	Pup	—
186	Female	Intact	8	Border collie	Pup	—
187	Female	Intact	4	Border collie	Pup	—
188	Female	Intact	5	Akita Inu	Pup	—
189	Female	Intact	8	Mix	Pup	—
190	Male	Intact	9	Hungarian vizsla	Pup	—
191	Female	Neutered	1	Mix	Pup	—
192	Male	Neutered	4	Mix	Pup	—
193	Female	Intact	1.5	Shetland sheepdog	Pup	—
194	Female	Neutered	4.5	English cocker spaniel	Pup	—
195	Female	Neutered	2	Mix	Pup	—
196	Female	Intact	2.5	Mix	Pup	—
197	Male	Neutered	2	Pug	Pup	—
198	Female	Neutered	5	Border collie	Pup	—
199	Male	Neutered	3	Border collie	Pup	—
200	Female	Neutered	9	Mix	Pup	—
201	Female	Neutered	5.5	Dogo Argentino	Pup	—
202	Male	Neutered	5	Briard	Pup	—

Table A1 (continued)

ID	Sex	Sexual state	Age (years)	Breed	Sound	Baby experience
203	Female	Intact	4	Dachshund	Pup	–
204	Male	Neutered	1.5	Mix	Pup	–
205	Male	Neutered	3	Mix	Pup	–
206	Male	Intact	2.5	Border collie	Pup	–
207	Female	Neutered	6	Mix	Pup	–
208	Female	Intact	7	Mix	Pup	–
209	Female	Neutered	1.5	Mix	Pup	–
210	Female	Intact	2	Aussie	Pup	–
211	Female	Intact	2	Mix	Pup	–
212	Male	Intact	0.5	Mix	Pup	–
213	Female	Neutered	0	Mix	Pup	–
214	Female	Intact	3	Papillon	Pup	–
215	Female	Intact	7	Kerry blue terrier	Pup	–
216	Female	Intact	1.5	Miniature pinscher	Pup	–
217	Female	Neutered	1	French bulldog	Pup	–
218	Male	Intact	1	Hungarian vizsla	Pup	–

Table A2

Effect of retesting on latencies

Latency	Test	Log likelihood	χ^2_1	$P(> \chi)$
Orient to owner	First	-937.49		
	Second	-937.47	0.024	0.877
Orient to speaker	First	-1894.70		
	Second	-1894.70	0.145	0.703
Listening	First	-2264.00		
	Second	-2263.10	1.831	0.176

Table A3

Effect of retesting on the principal component scores

	Test	Estimate	SE	df	t	Pr (> t)
Attention	(Intercept)	342.950	13.034	116.922	26.312	<0.001
	Retest	3.972	18.828	119.069	0.211	0.833
Owner	(Intercept)	0.601	0.012	116.626	50.405	<0.001
	Retest	-0.018	0.017	118.459	-1.063	0.290
Speaker	(Intercept)	0.878	0.007	117.442	125.278	<0.001
	Retest	-0.007	0.010	120.198	-0.661	0.510
Stress	(Intercept)	1.742	0.026	118.506	67.373	<0.001
	Retest	-0.020	0.037	122.556	-0.529	0.598

Table A4

Definitions of the acoustic parameters measured for each playback (NLPR was not defined in artificial calls)

Notation	Description
$f_{0\text{mean}}$	Mean fundamental frequency
$f_{0\text{max}}$	Maximum fundamental frequency
$f_{0\text{maxpozr}}$	Position of maximum fundamental frequency
$f_{0\text{min}}$	Minimum fundamental frequency
$f_{0\text{minpozr}}$	Position of minimum fundamental frequency
$f_{0\text{st}}$	Starting fundamental frequency
$f_{0\text{end}}$	Ending fundamental frequency
$f_{0\text{sd}}$	Standard deviation of the fundamental frequency
$f_{0\text{range}}$	Fundamental frequency range
$f_{0\text{chng}}$	Fundamental frequency change
CL	Mean call length
harmmean	Mean tonality
harmmax	Maximum tonality
harmdev	Standard deviation of tonality
Jitter	Mean variability/fluctuation of the f_0
Nonlinear phenomena ratio (NLPR)	Proportion of calls containing nonlinear phenomena
Entropy	Spectral flatness: the extent of the spectrum, describing the complexity of the sound (0=sine wave, 1=white noise)
Skewness	Skewness of the spectrum
Kurtosis	Kurtosis of the spectrum
Cmoment	Non-normalized skewness of the spectrum
centreofgravityfreq	Average height of frequencies in a spectrum

Table A5
Results of the PCA on the acoustic parameters

	Dominant pitch	Pitch_range	Tonality	Spectral_form	Pitch contour
Cmoment	0.934	-0.173	-0.034	-0.144	0.086
deviationfreq	0.921	-0.154	-0.063	-0.259	0.078
f_{min}	0.721	0.200	0.192	0.339	-0.064
Centrefofgravityfreq	0.714	0.355	0.112	-0.209	0.042
f_{ost}	0.579	0.337	0.150	0.329	-0.306
f_{orange}	-0.166	0.971	0.001	-0.136	0.036
f_{osd}	-0.118	0.956	-0.021	-0.155	0.059
f_{omax}	0.371	0.756	0.128	0.137	-0.019
f_{omean}	0.471	0.604	0.193	0.221	0.017
Harmmean	0.006	-0.067	0.894	0.143	-0.039
Harmmax	-0.012	-0.164	0.765	-0.215	0.090
Jitter	-0.115	0.020	-0.758	0.076	-0.029
Harmdev	-0.323	0.131	0.678	-0.227	0.070
Entropy	0.055	-0.267	-0.561	-0.261	0.141
Skewness	-0.159	-0.162	-0.050	0.900	0.085
Kurtosis	-0.128	-0.087	0.012	0.867	0.068
f_{ochng}	-0.034	0.232	0.026	0.068	0.869
f_{omnpozr}	-0.287	0.066	-0.082	-0.023	-0.772
f_{omxpozr}	-0.047	-0.042	-0.065	0.186	0.726
Sum of square loadings	3.733	3.339	2.877	2.258	2.045
Proportion of variance	0.196	0.176	0.151	0.119	0.108
Cumulative variance	0.196	0.372	0.524	0.642	0.750

The most important items within a component are in bold.

Table A6
Behaviour variable groups with variables and definitions

Variable	Definition	Type
Exploring		
Explore_speaker	Dog sniffs close to speaker (^a inside the drawn marker)	Duration (s)
Exploring_lab	Dog sniffs any surface of lab	Duration (s)
Orientation		
Orient_owner	Dog looks at the owner	Duration (s) Latency (s)
Orient_speaker	Dog looks towards location of hidden speaker	Duration (s) Latency (s)
Orient_door	Dog looks at door B (door between compartments)	Duration (s)
Others		
Listening	From start to end of playback dog shows alert behaviour towards location of speaker: head tilting, ear moving (changing position flicking back and forth, pricked forwards), mouth shut, appearing to listen	Duration (s)
Yawn	Dog yawns	Frequency
Touch_owner	Dog touches owner with its nose or legs	Duration (s)
Touch_speaker	Dog touches wall at the area where the speaker stands behind it	Duration (s)
Proximity		
Prox_owner	Dog is close to owner (inside the drawn marker)	Duration (s)
Prox_speaker	Dog is close to speaker (inside the drawn marker)	Duration (s)
Prox_door	Dog is close to door B (door between compartments, inside the drawn marker)	Duration (s)
Prox_exit	Dog is close to door A (where it entered with the owner, inside the drawn marker)	Duration (s)
Stand	Dog stands	Duration (s)
Moving		
Move	Dog runs, trots, walks, steps, changes position (sits down, stands up), jumps, etc.	Duration (s)
Sit	Dog sits	Duration (s)
Lie	Dog lies	Duration (s)
Vocalization		

Table A6 (continued)

Variable	Definition	Type
Bark	Dog makes short tonal sound	Duration (s)
Woof	Dog makes very short, soft, bark-like, but less tonal, sound	Duration (s)
Whine	Dog makes short or long high-pitched sound	Duration (s)
Growl	Dog makes long harsh sound	Duration (s)
Test markers		
Start	Start of test, measured from when door closes behind experimenter	Point
Stop	End of test, 30 s after last playback	Point
Sound_on	Start of playback (based on the spectrogram and sound)	Point
Sound_off	End of playback (based on the spectrogram and sound)	Point

^a Drawn marker: theoretical square around an object (owner's chair, speaker, door B, exit; see Fig. 1).

Table A7
Results of the PCA on the behavioural variables

	Attention	Stand	Owner	Speaker	Stress	Door
Orient_speaker	0.628	0.115	-0.132	0.347		-0.289
Explore_lab	-0.767	0.186	-0.234			-0.119
Listening	0.775	0.200			-0.138	
Move	-0.613	0.108	0.153	0.381		
Lie	0.192	-0.851	-0.120			
Stand	0.210	0.845		-0.106		
Bark			0.501	0.117	0.109	
Orient_owner			0.683			
Touch_owner		0.145	0.646		-0.221	-0.143
Woof			0.517	0.106	0.116	
Prox_speaker	0.142			0.798		
Explore_speaker	-0.168	-0.111		0.634		
Whine		-0.205	0.244		0.596	
Prox_owner	0.127	-0.203	0.191	-0.307	-0.574	-0.147
Prox_exit		0.123		-0.251	0.700	-0.194
Orient_door				-0.150	-0.147	0.782
Prox_door				0.203	0.163	0.657
Sum of square loadings	2.128	1.683	1.636	1.579	1.339	1.242
Proportion of variance	0.125	0.099	0.096	0.093	0.079	0.073
Cumulative variance	0.125	0.224	0.320	0.413	0.492	0.565

Table A8

Post hoc test on the pitch contour and playback number interaction on the stress component

Playback	Pitch contour	SE	df	Lower 95% CI	Upper 95% CI	Group
4	-0.020	0.028	644	-0.074	0.034	1
3	0.001	0.026	644	-0.050	0.05	12
1	0.066	0.025	644	0.016	0.116	2
2	0.072	0.023	644	0.028	0.117	2

CI: confidence interval. The last column indicates that the first and second playback differ significantly from the fourth, while the third does not.

Table A9

Post hoc test results of the effect of playback number on speaker orientation latency

	Exp(β)	Lower 95% CI	Upper 95% CI	z	P
1 vs 2	0.817	0.578	1.155	-1.845	0.252
1 vs 3	1.229	0.851	1.774	1.804	0.271
1 vs 4	1.559	1.197	2.031	3.766	0.001
2 vs 3	1.502	1.159	1.947	3.565	0.002
2 vs 4	1.908	1.378	2.642	5.472	<0.0001
3 vs 4	1.269	0.879	1.831	1.960	0.204

CI: confidence interval. Significant effects are in italics.

Table A10

Post hoc test results of the effect of playback number on the attention principal component

	β	SE	df	t	P
1 vs 2	27.9	9.84	648	2.837	0.024
1 vs 3	41.2	10.97	648	3.751	0.001
1 vs 4	71.9	11.35	648	6.331	<0.0001
2 vs 3	13.2	11.42	648	1.159	0.653
2 vs 4	43.9	11.79	648	3.728	0.001
3 vs 4	30.7	12.75	648	2.408	0.077

Significant effects are in italics.

Table A11

Post hoc test results of the effect of playback number on the owner principal component

	β	SE	df	T	P
1 vs 2	0.010	0.011	647	0.914	0.798
1 vs 3	0.030	0.011	647	2.703	0.036
1 vs 4	0.043	0.012	647	3.681	0.001
2 vs 3	0.020	0.011	647	1.783	0.283
2 vs 4	0.033	0.012	647	2.794	0.027
3 vs 4	0.013	0.012	647	1.075	0.705

Significant effects are in italics.

Table A12

Post hoc test results within the baby cry group: dogs experienced or inexperienced with babies

Contrast	Estimate	SE	Df	t	P
Experienced					
1 vs 2	3.25	9.87	162	0.329	0.988
1 vs 3	30.81	9.75	162	3.159	0.010
1 vs 4	45.56	10.30	162	4.421	0.001
2 vs 3	27.56	11.25	162	2.449	0.072
2 vs 4	42.30	11.73	162	3.606	0.002
3 vs 4	14.74	11.63	162	1.267	0.585
Inexperienced					
1 vs 2	3.19	13.77	162	0.232	0.996
1 vs 3	-10.85	13.61	162	-0.797	0.856
1 vs 4	13.52	14.38	162	0.940	0.783
2 vs 3	-14.04	15.70	162	-0.894	0.808
2 vs 4	10.33	16.37	162	0.631	0.922
3 vs 4	24.37	16.23	162	1.501	0.439

Significant effects are in italics.