Mother–lamb acoustic recognition in sheep: a frequency coding

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Ewes of the domestic sheep (*Ovis aries*) display selective maternal investment by restricting care to their own offspring and rejecting alien young. This trait relies on individual recognition processes between ewes and lambs. Whereas identification at the udder is only olfactory, distance recognition is performed through visual and acoustic cues. We studied the effectiveness and modalities of mutual acoustic recognition between ewes and lambs by spectrographic analysis of their vocal signatures and by playbacks of modified calls in the field. Our results show that ewes and their lambs can recognize each other based solely on their calls. The coding of identity within the vocal signatures, previously unknown in sheep, is similar in lamb and ewe: it uses the mean frequency and the spectral energy distribution of the call, namely the timbre of the call. These results point out a simple signature system in sheep that uses only the frequency domain. This engenders a signal with low information content, as opposed to some highly social birds and mammal species that may integrate information both in the temporal and spectral domains. The simplicity of this system is linked to the roles played by vision and olfaction that corroborate the information brought by the vocal signature.

Keywords: parent–offspring recognition; vocal signature; sheep; *Ovis aries*; playback experiments

1. INTRODUCTION

Maternal care in many species is selectively directed towards the mother's own young. This limits maternal energetic expenditure and ensures the fitness of breeders (Trivers 1972). In gregarious mammals, mother–offspring recognition is necessary to elicit well-directed maternal care. This recognition process involves sensory cues such as vision, olfaction and audition. The relative involvement of these modalities in parent–offspring recognition differs among species (Halpin 1991) and has been particularly well studied in sheep (*Ovis aries*). In this species, different modalities appear to be involved according to the distance range of the recognition process. Olfactory cues emitted by neonates are first learned by the ewe within a few minutes after birth (Smith *et al.* 1966; Morgan *et al.* 1975; Shillito-Walser & Alexander 1980; Klopfer 1996). These cues allow recognition at short range and permit the ewe to check the young's identity before allowing suckling. Such selective suckling behaviour was reduced in ewes that were made anosmic before lambing (Baldwin & Shillito 1974; Morgan *et al.* 1975; Poindron 1976; Ferreira *et al.* 2000). However, olfaction ceases to be efficient at distances greater than 0.25 m (Alexander & Shillito 1977; Alexander 1978; Shillito-Walser & Alexander 1980). Further studies using T-mazes and playback experiments have demonstrated the importance of both vision and audition in lamb recognition at longer distances (Lindsay & Fletcher 1968; Poindron & Carrick 1976; Shillito-Walser *et al.* 1981; Terrazas *et al.* 1999; Ferreira *et al.* 2000). Accordingly, two types of recognition of the lamb by the mother can be observed: a long-distance recognition using visual and/or acoustic cues permits the location of the young, whereas a close-range recognition made by

olfactory examination of the lamb allows a final check before allowing it to suckle. Acoustic, visual and olfactory recognition are achievable as early as 24 h *post partum* (Terrazas *et al.* 1999) and appear to be both independent and complementary, as each signal taken alone allows discrimination of the lamb by the ewe. However, the efficiency of visual cues might be reduced by distance and by the potential gathering of lambs into large groups. Because acoustic signals are efficient over long and short distances, acoustic cues appear to be fundamental in distal recognition.

Playback experiments have shown that the lamb's call constitutes a vocal signature that is recognized by the ewe (Shillito-Walser *et al.* 1981). However, the acoustic parameters that provide information about identity are currently unknown. Moreover, identification is a two-way process (Shillito & Alexander 1975; Terrazas *et al.* 2002), but recognition of the ewe by the lamb has scarcely been studied and no playback experiment has given evidence demonstrating acoustic recognition of the mother by the lamb (Arnold *et al.* 1975; Alexander 1977; Shillito-Walser & Alexander 1980).

The aim of this research was to investigate individual acoustic recognition between ewes and lambs and to identify the acoustic parameters in both calls that allow individual recognition. First, we performed an extensive analysis of both the temporal and the spectral patterns of the calls of lambs and ewes, to determine which pattern was likely to be more informative for individual recognition. Second, we performed playback experiments of modified signals to lambs and ewes to ascertain whether these parameters were actually important in acoustic recognition.

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Proc. R. Soc. Lond. B (2003) **270**, 1765–1771
DOI 10.1098/rspb.2003.2442

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2. MATERIAL AND METHODS

(a) Study subjects

Recordings and playback experiments were performed on 30 Tarasconnaises × Ile-de-France ewes and 42 lambs from a Pyrenean farm at Argein (Ariège, France), during the first two weeks of September 2001 and 2002. No particular method was used to induce oestrus, and the age of the studied lambs varied between 3 days and two weeks. All animals were tagged on the ear with a number that allowed individual identification.

(b) Recording procedure

Each lamb was caught and placed in a small 1 m² pen outside the sheepfold while its mother stayed nearby. Vocalizations exchanged between mother and lamb were then recorded using a Sony TCD10 Pro II DAT (frequency response flat within the range 20–20 000 Hz) and a unidirectional Shure SM57 dynamic microphone (frequency response 100–20 000 Hz at ± 3 dB). The distance between the microphone and the head of the recorded animal was *ca*. 50 cm.

(c) Signal acquisition and analysis

Calls were digitized with a 16-bit acquisition card at 44 100 Hz sample rate, using COOL EDIT acquisition software. We analysed 225 calls from 15 ewes and 225 calls from 15 lambs (15 calls per individual).

To characterize the acoustic structure of the calls, we measured nine parameters describing spectral density of the call and temporal patterning of amplitude and frequency parameters (figure 1). To describe the spectral density of the call, we calculated a power spectral density on the total length of the call using Welch's averaged, modified periodogram method (Welch 1967). To describe the call in the frequency versus time domain, we measured the frequency modulations of the call by means of software specifically written for that purpose, based on the autocorrelation method associated with filtration of the signal. Calculations resulted in a vector of 17–157 measurements, depending on the duration of the call. We used this frequency contour to calculate the mean (F_{mean}), initial (F_{start}), final (F_{end}), minimal (F_{min}) and maximal (F_{max}) frequencies. Because we found a strong correlation between the mean frequency and the four variables just mentioned, we expressed them relative to the mean frequency (table 1). Amplitude modulation over time was measured from the envelope of the sound, calculated by the analytical signal calculation (Mbu-Nyamsi *et al.* 1993). The duration of the call was measured from the envelope.

We then examined individual variation in the calls of lambs and ewes to determine which parameters were the most efficient for coding individual identity. This efficiency was measured using a stereotypy index (H_S) based on information theory (Shannon & Weaver 1949), as described in the information analysis method developed by Beecher (1989). The higher the values of its information content H_S, the more potential a given parameter has for encoding individual identity. Mathematical formulations of the H_S index are given in Appendix A. The sound measurements and spectral analysis were done with SCILAB software, and statistical analyses were performed by using a SYSTAT package.

(d) Playback procedure

We played back ewes' calls to 42 lambs and lambs' calls to 30 ewes when the mothers were taken outside to graze. Animals were tested individually. Tests were performed during the afternoon when ewes were separated from their lambs and taken to a distant field to graze. Tested ewes were enclosed in a 300 m² field, and tested lambs were gathered in a 10 m² pen in the sheepfold. Playback experiments were performed at least half an hour after the ewes' arrival in the field or the lambs' enclosure in the holding pen. This allowed the animals to become habituated to the testing conditions. The broadcast chain consisted of a Sony TCD10 Pro II DAT connected to an autonomous MA-101 Mipro amplifier loudspeaker (27 W, frequency range 50–18 000 Hz ± 3 dB). The loudspeaker was placed *ca*. 10 m away from the tested ewes, and 2 m away from the lambs. In both cases, the experimenters were out of sight of the animals.

Each playback sequence consisted of four signals separated by 4 s of silence. A non-modified sequence consisted of four different calls from the same animal, and modifications were made similarly on each of these four calls. Each tested individual was subjected to three playback sequences, played in random order: non-modified calls of its mother or young (hereafter referred to as 'kin calls'), same calls but modified, and unmodified calls of another unrelated ewe or lamb from the same flock (hereafter referred to as 'strangers' calls'). All animals from the flock were gathered into the sheepfold every day and night, from evening to early afternoon. During this period, numerous vocalizations were exchanged between ewes and lambs. We therefore assumed that strangers' calls were familiar to the tested individuals. Each broadcast was separated from the others by at least 15 min. Hence the observed responses of the tested animals were neither a result of cumulative excitation nor dependent on playback order. Behavioural responses of tested animals to playbacks consisted of head turns, body orientation towards the source of the sound, calls in reply and occasionally movement towards the loudspeaker. To evaluate the intensity of the responses, we measured the number of calls emitted in reply during 1 minute after the playback. This call rate was shown in a previous study to be positively correlated with recognition (Shillito-Walser *et al.* 1981).

In a first step, the responses obtained with non-modified kin calls were compared with those induced by strangers' calls. This allowed testing of the efficiency of acoustic recognition. As each individual was tested several times and did not show the same response to playbacks at different times, we calculated the mean response for each individual. We compared those means between playbacks of non-modified kin calls and of strangers' calls using a Wilcoxon signed-ranks test.

Second, we tested the effects of modifications of the kin calls on the animals' responses. Modifications were designed to test the relative importance of frequency and temporal parameters in individual recognition. We broadcast two kinds of experimental signal:

(i) Time-reversed calls: in these signals, the temporal parameters (amplitude and frequency modulations) were modified but the frequency parameters were preserved.
(ii) Frequency-shifted calls: in these signals the fundamental frequency was randomly lowered or increased by 50 Hz by repeating or removing periods of the signal, followed by resampling. Here, the temporal parameters are preserved but the frequency and the spectral density of the calls are modified.

Each modified signal was further rescaled to match the root-mean-squared amplitude of the reference signal. This allowed both the control and the modified signals to have the same output level. Modifications were performed by using COOL EDIT software.
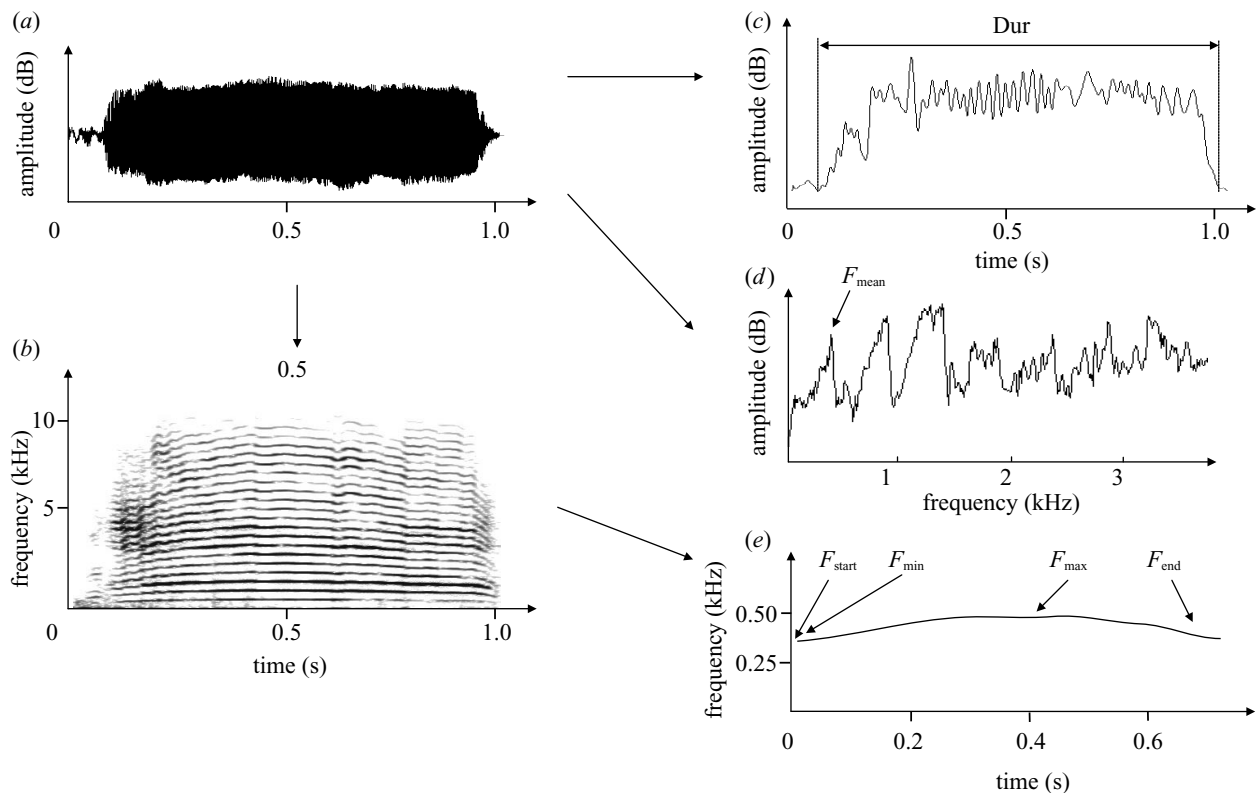
Figure 1. Analysis of acoustic parameters of lambs' and ewes' calls: example of a lamb's call. (*a*) Oscillogram and (*b*) spectrogram of a lamb's call (window size 512 points). (*c*) Amplitude envelope calculated from the oscillogram (temporal resolution of 5.8 ms). We used the envelope to calculate the total duration of the call (Dur). (*d*) Average power spectrum (Welch's average periodogram, Hanning window with frame length of 1024 points, frequency resolution 21.5 Hz). (*e*) Modulation of the fundamental frequency during the call. Frequency modulation was calculated by using 75% overlapping spectrograms (Hanning window, window size of 1024 points, frequency resolution of 21.53 Hz, temporal resolution of 11.6 ms) by means of software written for that purpose, based on the auto-correlation method associated with filtration of the signal. We used this frequency contour to calculate the mean, initial, final, minimal and maximal frequencies (F_{mean}, F_{start}, F_{end}, F_{min}, F_{max}).

For each playback experiment, we obtained three measures: response of the animal to the kin calls, to the modified calls and to the alien calls. When individuals did not respond to the kin calls they did not respond to the modified calls either. To check how modifications impaired recognition, we included in our analysis only those trials where the response to the kin calls during the same playback experiment was positive. Each modified signal was tested only once on each individual to prevent pseudoreplication. For each modification, we compared responses to modified calls with responses to kin calls and with responses to alien calls, using Wilcoxon signed-ranks tests. We also compared ewes' and lambs' responses for each playback (kin call, alien call, modified call) with a Mann–Whitney *U*-test.

3. RESULTS

(a) *Analysis of the calls*

Results of the analysis are shown in table 1. Stereotypy analysis of the calls revealed that ewes' and lambs' calls showed a basis for individual recognition, as six and eight parameters, respectively, out of nine proved discriminant (ANOVA tests, $p < 0.01$; see table 1). For both ewes and lambs, the most discriminant parameters are the duration of the calls, the mean frequency and the spectral density. The temporal variables, represented here by modulations of frequency and amplitude over time, displayed a low

information capacity. Frequency modulations were not discriminant; a closer analysis showed that they were actually very weak, as the mean values of $RelF_{max}$, $RelF_{min}$, $RelF_{start}$ and $RelF_{end}$ were all close to one. These values also have a low information capacity, indicating that the range of frequency during the call is not stereotyped.

(b) *Playback experiments*

Playbacks of non-modified signals showed that kin calls induced significantly more calls in reply than alien calls (Wilcoxon signed-ranks test: ewes' responses: $Z = -3.66$, $N = 30$, $p < 0.001$; lambs' responses: $Z = -4.69$, $N = 42$, $p < 0.001$). Ewes and lambs can recognize their mother or young based on their call. However, the proportion of positive responses significantly decreased in relation to the number of playbacks performed on each individual (Kruskal–Wallis test; for ewes: $H = 28.31$, $p < 0.001$; for lambs: $H = 28.35$, $p < 0.001$) and after the sixth experiment the animals did not respond any more to playbacks.

Responses to modified calls differed according to the way calls were modified (figure 2). For both ewes and lambs, reversed calls induced significantly more calls in reply than alien calls (Wilcoxon signed-ranks test; ewes' responses: $Z = -2.21$, $N = 10$, $p < 0.05$; lambs' responses: $Z = -3.06$, $N = 19$, $p < 0.005$). The number of calls in reply was slightly lower than for non-modified calls but this difference proved non-significant (Wilcoxon
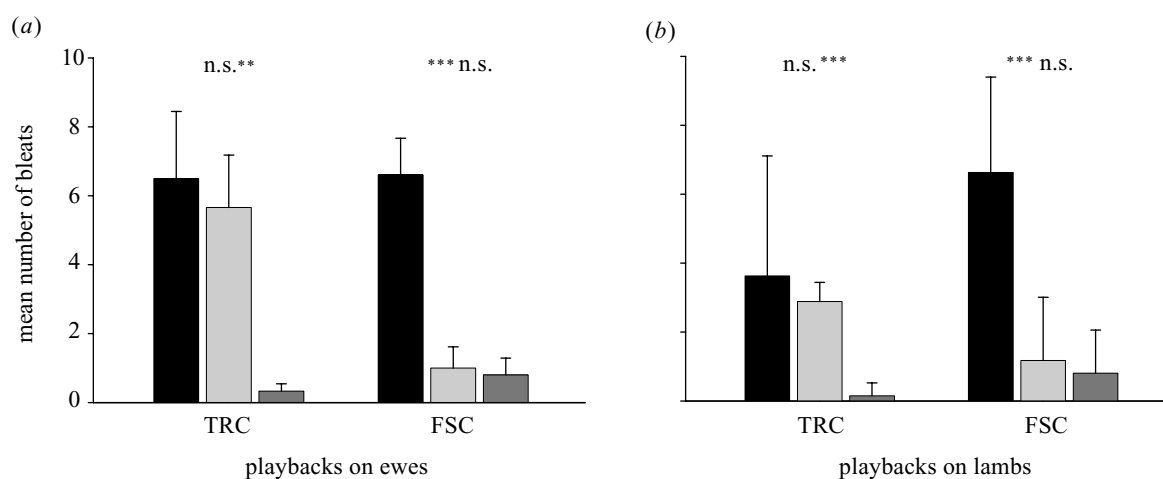
Figure 2. Results of playbacks of non-modified, modified and alien calls on (*a*) ewes' and (*b*) lambs' mean number of bleats (± s.e.m.) emitted during the first minute following the playback. Two kinds of modified calls (light-grey bars) were tested: time-reversed calls (TRC) and frequency-shifted calls (FSC). For each playback of a modified call, the replies to non-modified (black bars) and modified calls were recorded as well. Comparisons between responses to non-modified and modified calls, and between responses to modified and alien (dark-grey bars) calls were made by using a Wilcoxon signed-ranks test. Degrees of significance are shown above the bars: $^{***}p < 0.005$; $^{**}p < 0.05$; n.s., not significant.

signed-ranks test; ewes' responses: $Z = -0.41$, $N = 10$, $p > 0.05$; lambs' responses: $Z = -1.66$, $N = 19$, $p > 0.05$). Time reversal of the calls did not alter individual recognition in ewes or in lambs. However, frequency-shifted calls did induce significantly fewer replies than non-modified calls (Wilcoxon signed-ranks test; ewes' responses: $Z = -2.81$, $N = 10$, $p < 0.005$; lambs' responses: $Z = -2.94$, $N = 11$, $p < 0.005$), and no significant difference was found with responses to alien calls (Wilcoxon signed-ranks test; ewes' responses: $Z = -0.71$, $N = 10$, $p > 0.05$; lambs' responses: $Z = -0.96$, $N = 11$, $p > 0.05$). Frequency-shifted calls were not recognized by ewes or lambs. Comparisons between ewes' and lambs' responses to kin, alien, time-reversed or frequency-shifted calls revealed no significant difference for any playback (Mann–Whitney *U*-tests; $p > 0.05$ for all tests).

4. DISCUSSION

Although several studies have investigated acoustic recognition in sheep, so far none has examined the actual modalities of this process. In this study, we use spectrographic analysis and playback experiments to demonstrate that both lambs and ewes can discriminate between their own mother or young and a stranger based solely on its call, and that this recognition process is made through the spectral content of the calls.

In a first step, the stereotypy analysis of the calls showed that both ewes' and lambs' calls are individually distinctive. The information capacity values single out three parameters as discriminant: the duration, the spectral density and the mean fundamental frequency of the call. Temporal parameters such as frequency and amplitude modulations are not stereotyped. These results show a strong potential for a frequency coding of identity in sheep, using the spectral profile and pitch of the calls.

Our playback experiments confirmed in a second step that these coding potentialities are actually used in individual recognition of both lambs and ewes. First, playbacks of non-modified signals showed that ewes and lambs

are equally able to discriminate between alien and kin based on their calls. As strangers' calls were assumed familiar to the tested individuals, this result gives good evidence for individual vocal recognition between lamb and ewe, and confirms that recognition between mother and lamb over long distances is actually a two-way process. Previous playback experiments have already provided evidence for ewes' recognition of lambs' calls (Poindron & Carrick 1976; Shillito-Walser *et al.* 1981). However, only recognition of the lamb by its mother had been tested that way. Recognition of ewes by lambs has only been assessed by suppression of either acoustic or visual cues during choice tests (Arnold *et al.* 1975; Shillito & Alexander 1975; Alexander & Shillito 1977). This is the first report of mothers' voice recognition by lambs that uses actual playback experiments. Because our study involved no enclosures or capture and release of animals, our experimental design also reduced any potential stress that could alter the animals' behaviour. Although an overall significant difference was found between responses to kin and alien calls, playbacks of kin calls did not always induce a positive response. The lack of reaction to kin calls is probably because of a low motivation of the animals to find their mother or young, as our experiments were performed in conditions where ewes and lambs were routinely separated for several hours every day. The percentage of positive responses significantly decreased as well with the number of tests, presumably as animals became accustomed to the tests. Previous experiments have also shown that the stimulus offered by the presence of a 'model' lamb increased the response of ewes to playbacks (Shillito-Walser *et al.* 1981). During our playbacks, no ewe or lamb was in sight of the tested animals (respectively lambs or ewes). Although our results confirm that the acoustic stimulus alone can allow identification, it is likely that a visual stimulus may enhance the efficiency of recognition. This is consistent with previous experiments assessing the relative importance of vision and hearing in mother–lamb recognition, which established that both sensory cues are sufficient for identification but that the efficiency of recog-

Table 1. Analysis of acoustic parameters of ewes' and lambs' vocal signatures (15 individuals, 15 calls for each individual).

(Abbreviations: Dur, duration of the call; F_{mean}, mean value of the fundamental frequency; $RelF_{start}$, relative starting frequency (= F_{start}/F_{mean}); $RelF_{end}$, relative ending frequency; $RelF_{min}$, relative minimal frequency; $RelF_{max}$, relative maximal frequency; H, information capacity (H_{est} for the three first vectorial parameters and H_s for the last six scalar parameters); we used ANOVAs to test the difference between individuals: ***$p < 0.001$; **$p < 0.01$; n.s., not significant).

| | ewes' vocal signature | | | | lambs' vocal signature | | | |
| | | ANOVA | | | | ANOVA | | |
variables	mean ± s.d.	$F_{14,210}$	p	H	mean ± s.d.	$F_{14,210}$	p	H
spectral density	—	9.26	***	0.32	—	11.66	***	0.39
frequency modulation	—	1.69	n.s.	—	—	2.06	n.s.	—
amplitude modulation	—	4.65	***	0.16	—	4.78	***	0.16
Dur (s)	0.79 ± 0.23	8.29	***	0.29	0.71 ± 0.22	17.51	***	0.54
F_{mean} (Hz)	152 ± 15.4	7.84	***	0.27	345 ± 49.6	16.80	***	0.53
$RelF_{start}$	0.99 ± 0.03	1.45	n.s.	—	0.89 ± 0.10	2.82	**	0.09
$RelF_{end}$	1.00 ± 0.03	1.49	n.s.	—	0.93 ± 0.11	3.70	***	0.12
$RelF_{min}$	0.96 ± 0.01	2.51	**	0.07	0.84 ± 0.08	3.26	***	0.11
$RelF_{max}$	1.04 ± 0.01	4.37	***	0.15	1.08 ± 0.04	2.78	**	0.08

nition is lowered when only one cue is available (Arnold *et al.* 1975; Alexander 1977; Alexander & Shillito 1977; Shillito-Walser 1978). Visual contact in particular seems to act as a stimulus that enhances a searching behaviour of the ewe or the lamb.

Second, playbacks of modified signals showed which call parameters actually conveyed information on identity. Theoretically, information can be extracted from an acoustic signal using two main processes (Okanoya & Dooling 1991): (i) integration in the frequency domain, using a power spectral profile; (ii) integration in the temporal domain, using a combination of elements in the signal or using the structure of single elements. In our experiments, ewes and lambs correctly recognized reversed calls, modified in the temporal domain, whereas frequency-shifted calls induced no more responses than alien calls. These experiments support the results of our stereotypy analysis, and both show that the coding of identity in lambs' and ewes' calls is similar and is made throughout the spectral profile and pitch of the calls. Identification is therefore not based on the evolution of a parameter over time but rather uses a one-dimensional parameter obtained from a frequency analysis of the whole signal, namely the timbre of the call. Interestingly, the call duration, which is highly discriminant between individuals, is none the less of lesser importance in recognition, as frequency-shifted parameters whose duration is unchanged are not recognized. The high stereotypy of this parameter may be an artefact, given that most calls were recorded through a sole session per individual. The duration of the call might be correlated here to the emotional state of the animal and therefore may not represent a good recognition cue.

Coding in the frequency or in the temporal domain is not equivalent in efficiency. Frequency analysis is known to be slow in a physical sense (Beecher 1988) as well as physiologically (Bregman 1978): when the duration of the analysis decreases, the uncertainty in the measurement of frequency increases. Accurate analysis of frequency is more time consuming than analysis in the time-domain. However, modulation in time is difficult to produce (Brackenbury 1982), and requires a high degree of control

of the sound source. Our research shows that the sheep's vocal signature is based on the simpler, but less efficient, frequency-coding system. An overview of the different recognition systems found in highly social birds and mammals suggests that coding in the temporal domain, which is efficient but costly, is favoured in situations where the possibilities for confusion are high. An extremely confusing context is actually given by large colonies of birds. In very large and dense colonies, only acoustic cues can convey information for individual recognition. Moreover, parent–offspring separations are frequent and long lasting, which is not the case in mammals. In penguins of the genus *Aptenodytes*, the situation is even more confusing as no topographical cue such as a nest helps recognition. In these species, it has been found that the signature system is highly sophisticated and based on a combination of spectral and temporal parameters (Aubin & Jouventin 2002). However, among penguins these complex signatures are unique to the large king and emperor penguins in the genus *Aptenodytes*. Other penguins, which can also rely on topographical cues to find each other, have been shown to use simpler systems based on the harmonic content of the call (Aubin & Jouventin 2002; Jouventin & Aubin 2002). In mammals, such aggregated contexts are less common. Bats and bottlenose dolphins, which are not helped by visual or topographical cues, also use accurate frequency contours as signatures (Caldwell *et al.* 1990; Scherrer & Wilkinson 1993). In those cases, however, the possibilities for confusion are reduced owing to the use of olfaction by bats, and to a low number of individuals in dolphin pods. Olfaction is used by fur seals as it is by sheep, as a final check of the young's identity. However, young fur seals are left alone for long periods in large colonies, and visual cues may be less reliable as seals suffer from astigmatism on land (King 1983). In this more confusing context, the discrimination capacity of the signal is increased through a combination of spectral characteristics and of a very simple temporal frequency pattern (Charrier *et al.* 2002).

In sheep, mother–lamb recognition is a multimodal process, where sound and vision bring redundant and complementary information that is finally checked at close

quarters by olfaction. This situation presents an ultimate case where confusion is considerably reduced, probably even impeded through domestication. Our finding of a frequency coding in mother–lamb recognition supports the hypothesis of simpler coding systems when the probability of misdirected parental care is lower. Such a pattern occurs independently of systematics, as convergent systems can be found in both birds and mammals. Further studies of acoustic recognition in other ungulates would be useful to generalize this hypothesis to other terrestrial mammals.

APPENDIX A

Information capacity measurements give a quantitative estimate of a given parameter's efficiency in recognition. Our measured parameters were divided into scalar and vectorial parameters. Analysis of scalar parameters was made by using the information analysis method developed by Beecher (1989). A one-way ANOVA was first carried out on each variable. Only variables giving a significant F ($p < 0.05$) were considered. The information content of one variable (H_S) was calculated from the F value found in the ANOVA. H_S, measured in bits per signal, represents the number of binary decisions necessary to discriminate among N objects. For a given variable, H_S is expressed as:

$$H_S = \log_2 \sqrt{\frac{\sigma_B^2 + \sigma_W^2}{\sigma_W^2}} = \log_2 \sqrt{\frac{F + n - 1}{n}},$$

where n is the number of calls per individual. H_S is derived from the F value found in the ANOVA, but, unlike F, does not vary with sample size. Information capacity measurements are therefore more reliable to compare variables and samples. The information analysis we used does not require that the signal systems be compared in the same units (Beecher 1989). The unitless nature of the information measures derives from standardizing the variables by dividing through by the within-individual standard variation. Direct comparisons of the individual acoustic variables were thus appropriate.

Vectorial parameters were compared between calls by using a variant from the previous expression of H_S. We used a distance index d_{Aij} as an assessment of the square distance between two given vectors of measurements $A_i(t)$ and $A_j(t)$:

$$d_{Aij} = \frac{1}{N_{min}} \sum_{k=1}^{N_{min}} (A_j(k) - A_i(k))^2,$$

N_{min} being the shortest length of the two vectors. In a group of k observations, the sum of distance indices between all pairs of observations (dist) can be estimated using the sum of square (SS):

$$\text{dist} = \sum_{i,j} d_{Aij} = k \times \sum_j (A_j - \bar{A})^2 = k.\text{SS}.$$

Consequently, the information capacity H_S for g groups with n observations per group was estimated as follows:

$$H_{est} = \log_2 \sqrt{\frac{F_{est} + n - 1}{n}},$$

where

$$F_{est} = \frac{n-1}{g-1} \left(\frac{\text{dist}_T - g \times \text{dist}_W}{\text{dist}_W} \right),$$

dist$_T$ being the sum of distance indices between all pairs of calls, and dist$_W$ the sum of distance indices between pair of calls within each individual.

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