ANIMAL BEHAVIOUR, 2003, **65**, 543–550
doi:10.1006/anbe.2003.2073

Vocal signature recognition of mothers by fur seal pups

ISABELLE CHARRIER*†, NICOLAS MATHEVON*‡ & PIERRE JOUVENTIN†
*Laboratoire de Biologie Animale, Université Jean Monnet
†CEFE-CNRS UPR 9056, Montpellier
‡NAMC-CNRS UMR 8620, Université Paris-Sud, France

*(Received 8 February 2002; initial acceptance 19 March 2002;
final acceptance 21 July 2002; MS. number: 7225R)*

Subantarctic fur seals, *Arctocephalus tropicalis*, come ashore to breed in dense colonies and lactating females have to alternate foraging trips at sea with periods ashore during which they suckle their pups. The effectiveness of vocal recognition between mothers and pups, has been shown experimentally. To see whether the recognition abilities of females differ from those of their offspring, we investigated how pups recognize their mother's calls. We used artificially modified signals in playback experiments to determine which acoustic parameters support the recognition process. Pups used both the energy spectrum and the ascending frequency modulation occurring at the beginning of each call. However, they seemed to rely mainly on spectral analyses. The vocal identification process at a perceptual level is therefore asymmetrical, as mothers mainly use temporal structures to recognize their pup's calls.

In social bird and mammal species, parents and offspring develop the ability to identify each other (Halliday 1983), with mutual fitness benefits (Trivers 1974; McArthur 1982). For parents, offspring recognition prevents misdirected parental care, limits their expenditure of energy, and ensures their reproductive success. For young animals, recognition of parents is essential to their survival since in most social or colonial species parents feed only their own offspring. There is evidence that parent–offspring recognition is especially important for colonial species, with the degree of recognition (i.e. mutual or unilateral recognition) seeming to vary between species and depending on environmental constraints (Halliday 1983).

Some studies have experimentally investigated the sensory modalities supporting individual recognition between parents and offspring, and have shown that identification relies mainly on vocal and/or olfactory signals. Acoustic cues have been well studied in colonial birds (e.g. penguins: Jouventin et al. 1999; Lengagne et al. 2000; Aubin & Jouventin 2002; gulls: Charrier et al. 2001a; swallows: Beecher et al. 1981) but few studies have investigated the fine acoustic processes (information coding/decoding) underlying vocal individual recognition in mammals. In this respect, otariids are a good model to explore these mechanisms, because their vocal recognition has been widely observed and experimentally demonstrated (Trillmich 1981; Insley 1992, 2000; Charrier et al. 2001b).

Otariids breed in large dense colonies. After parturition, females take care of their pups for several months, alternating foraging periods at sea, during which pups are left alone in the colony, with periods ashore for the purpose of suckling. Because females do not feed nonoffspring (Boness 1990; Georges et al. 1999), and mother and pup are frequently separated, effective individual recognition between mother and offspring is vital for finding each other among several hundred conspecifics (Riedman 1990). Although this recognition may rely on several sensory modalities, vocal recognition is a key factor as shown by playback experiments in the Galapagos fur seal, *Arctocephalus galapagoensis* (Trillmich 1981), subantarctic fur seal, *Arctocephalus tropicalis* (Charrier et al. 2001b, 2002a), and northern fur seal, *Callorhinus ursinus* (Insley 2000, 2001).

In a study on northern fur seals, Insley (2001) showed that the effectiveness of acoustic recognition seems to differ between the female and her pup. In response to playback, pups are more vocally responsive than mothers and sometimes make recognition errors by responding to another female's calls. In contrast, females respond strongly only to the call of their own pup. From an evolutionary point of view,

Correspondence and present address: N. Mathevon, Laboratoire de Biologie Animale, 23 rue Michelon, Université Jean Monnet, 42023 St Etienne cedex 02, France (email: mathevon@univ-st-etienne.fr). I. Charrier is now at the Department of Psychology, University of Alberta, Edmonton, AB T6G 2E9, Canada. P. Jouventin is at CEFE CNRS UPR 9056, 1919, route de Mende, 34293 Montpellier cedex 5, France.

0003–3472/02/$30.00/0

parent–offspring conflict theory emphasizes that the selection pressures acting on mothers and pups are different (Trivers 1974). Recognition is crucial to the pups' survival, whereas an error in recognition represents a smaller cost for adult females; therefore, for pups selection may favour probing and deception, and necessitates a more liberal acceptance criterion (Insley 2001). This behavioural asymmetry may have different causes, for example are the pups' 'errors' linked to a difference in motivation or in recognition ability? No clear answer is available to this question.

In the subantarctic fur seal, pups are exposed to frequent absences of 2–3 weeks when their mothers are foraging at sea (Georges & Guinet 2000). The first separation between mother and pup occurs very early, some 2–8 days after parturition. We have shown that pups are able to recognize their mother's calls before her first sea trip (Charrier et al. 2001b). Females are also able to identify their pup's calls. This mutual recognition system is very effective: when the mother returns, she is reunited with her pup in less than 7 min (Charrier et al. 2001b). Because of the strong socioecological constraints, it is likely that natural selection has led to special adaptations for improved recognition. In a long-term study on this species, we examined whether there are differences, such as asymmetry, in the recognition abilities of both females and their offspring.

In a previous paper, we investigated which call characteristics fur seal mothers use to identify their pups (Charrier et al. 2002a). It appears that mothers rely on several acoustic parameters; the main one is the frequency modulation of the pup's call, but the energy distribution of the spectrum plays a lesser role in the decoding process. In this paper, we report an investigation of how pups recognize their mother's call. We used artificially modified signals to determine which acoustic parameters support the recognition process. We then compared these results with those obtained with the mother, and assessed the extent to which pup's and female's recognition processes differ.

METHODS

Study Location and Animals

We studied subantarctic fur seals breeding on Amsterdam Island (37°55′S, 77°30′E), Indian Ocean, from February to June 2000. The colony comprises between 500 and 550 mother–pup pairs. The fur seals are accustomed to seeing humans and are not disturbed by their presence. Females have been tagged for several years, and their pups were marked shortly after birth with temporary labels glued on to their fur. At ca. 1 month old, each pup was double tagged in the web of the foreflippers with an individually numbered plastic tag (3 × 1 cm; Dalton Rototags, Dalton Supply, Nettlebed, U.K.). Tagging lasted less than 1 min and did not cause any injury or infection. This method is commonly used by researchers in mammal experiments (Georges & Guinet 2000). The study was approved by the Ethical Committee of the French Polar Institute (IPEV).

Recordings and Signal Acquisition

To record the Pup Attraction Calls of females (Fig. 1a), which the pup uses to recognize its mother (Paulian 1964), we used an omnidirectional Revox M 3500 microphone (frequency bandwidth 150–18 000 Hz ± 1 dB) mounted on a 2-m boom and connected to a Sony TC-D5M audiotape recorder. Calls were recorded when a female and her pup were searching for each other, for example when she returned from a feeding trip or from a short swim. During the recordings, the distance between the mother and microphone was about 0.5 m. This short distance never disturbed the behaviour of the recorded female. Calls were digitized with a 16-bit acquisition card at 22 050 Hz sample rate, using acquisition software [Cool Edit, Syntrillium Software (http: www.syntrillium.com/)]. Signals were then stored on the hard disk of a PC computer.

Playbacks

Experimental signals were broadcast with a Sony TC-D5M tape recorder connected to an Audax unidirectional loudspeaker via a customized 10-W amplifier (frequency response 1–9 kHz ± 4 dB). The loudspeaker was placed 3–4 m from the pup being tested. Calls were played at natural rates (1 call/3 s) and at a natural sound pressure level (SPL=79 ± 5 dB measured at 1 m with a Bruël & Kjaer sound level meter type 2235). Tests were carried out during the mother's foraging trips. Because preliminary experiments showed that pups' responses are strongest and most mother specific between the 5th and the 9th day after the female's departure (Charrier et al., 2002b), we tested pups during this period. We noted the daily presence of each tested pup's mother. As a general rule, for a given pup and for a given experimental day (i.e. a playback session), we broadcast an experimental tape containing one experimental series (three identical modified signals, series duration: 10–15 s) and a control series (a succession of three natural calls from the mother, series duration: 10–15 s). Within a playback session, the two series were separated by at least 20 min. We also randomized the order of presentation of both series. To avoid habituation, there was always a minimum of 2 days between playback sessions and a given pup was not tested more than once with a given experimental series. To prevent pseudoreplication, calls of the control series were different for each playback session of a given pup (McGregor et al. 1992). Playback tests were carried out on a sample of 47 pups. The maximum number of playback sessions for a given pup was six.

Criteria of Response

Under natural conditions, a female's calls elicited the following stereotypical response by her young: calling, searching head movements (looking around) and approach. Before broadcasting an experimental series, we observed the pup for 2 min. Then during playback we noted any change in its behaviour. To characterize the

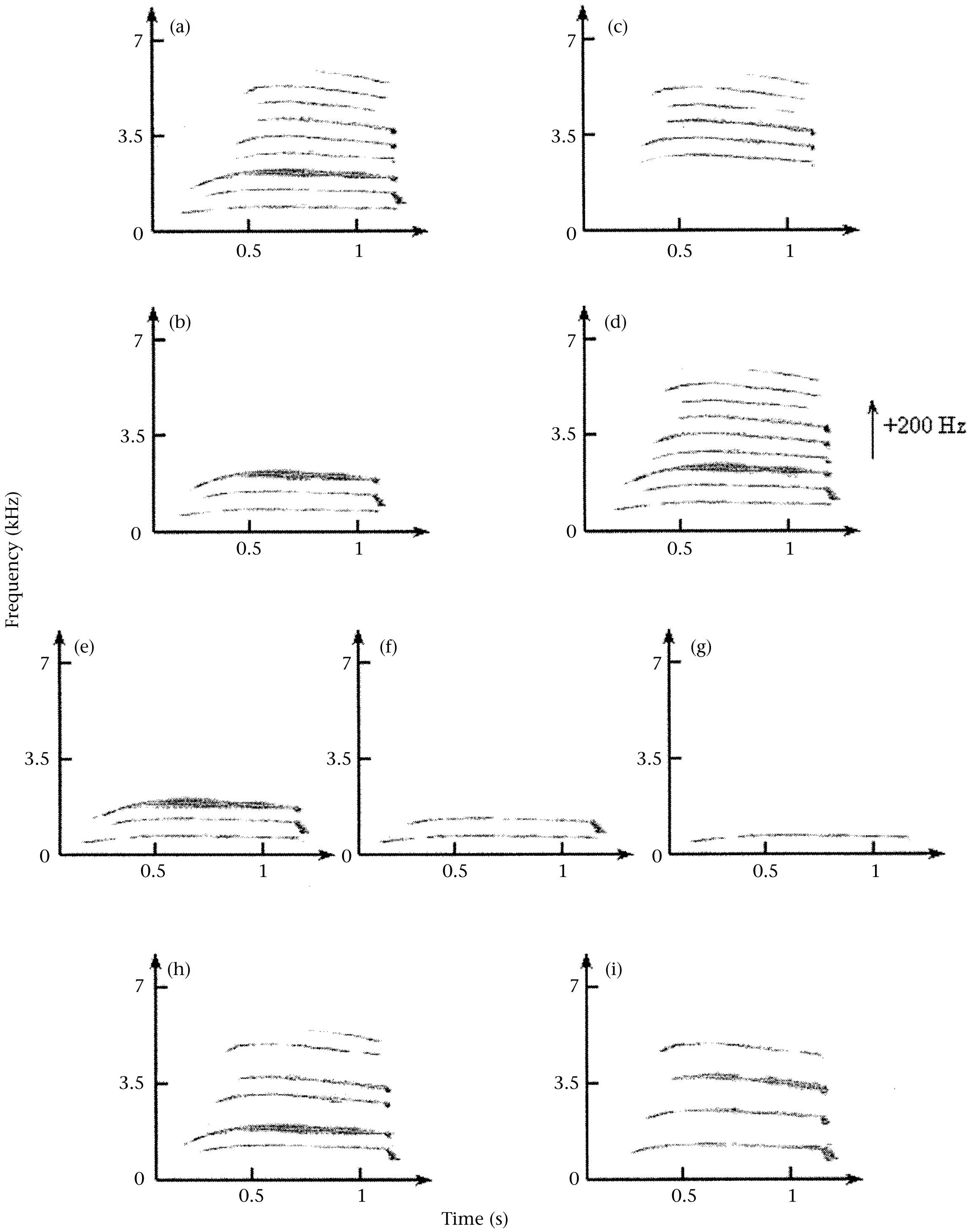

Figure 1. Spectrograms of a female's call modified in the frequency domain as used in playback experiments to pups. (a) Control signal, (b) low pass, (c) high pass, (d) example of shifted signal (+200 Hz), (e) fundamental frequency and its two first harmonics (Fo+H1+H2), (f) fundamental frequency and only the first harmonic (Fo+H1), (g) fundamental frequency only (Fo), (h) filter of one of three harmonics (1H/3), (i) filter of one of two harmonics (1H/2).

response of pups to playback signals, we used a three-point scale: (1) 0: no reaction; (2) 1: calls in response and/or searching head movements only during the playback; (3) 2: calls in response and/or searching head movements during and after the playback. Responses of class 0 correspond to no-response, showing absence of mother's call recognition, whereas responses of classes 1 and 2 correspond to positive responses and demonstrate mother's call recognition.

To compare the pups' responses to experimental and control signals we used a two-tailed Wilcoxon signed-ranks test (Sokal & Rohlf 1995).

Experimental Signals

Using natural mothers' calls (Fig. 1a), we created experimental signals by modifying these sounds in both the frequency and temporal domains. Because we were interested in the pups' recognition of the mother's call, we tested each pup with experimental signals prepared from its own mother's calls. To modify the natural calls we used the Syntana and Goldwave packages (Aubin 1994).

The Pup Attraction Call of females is a complex sound with a fundamental associated with its harmonic series (Charrier et al., 2003). In the temporal domain, it has three parts (Fig. 1a): an initial part with a rapid ascending frequency modulation, a central part with a weak or no frequency modulation, and the final part characterized by a descending frequency modulation. Given this acoustic structure, we made experimental signals as follows.

Modifications in the frequency domain

(1) To test whether the whole spectrum of call is required for recognition, we built low- and high-pass signals (Fig. 1b and 1c, respectively) by digital filtering (FFT window size: 4096, precision in frequency=5.4 Hz). As a general rule, a cutoff frequency of 1500–2000 Hz allows the spectral energy to be divided equally between the two signals. As calls are highly individualized, the cutoff frequency was different for each female's calls but was always constrained within this frequency interval (1500–2000 Hz). RMS (root mean square) values of both experimental signals were adjusted to that of the natural signal. The low-pass signals were composed of the fundamental frequency and their two to four first harmonics (the number of harmonics was different for each female and dependent on the fundamental frequency value).

(2) To assess the minimal number of harmonics the pup required to recognize its mother, we filtered the natural female calls using digital filtering (FFT window size: 4096, precision in frequency=5.4 Hz). The first experimental signal was composed of the fundamental frequency and its two first harmonics (Fo+H1+H2, Fig. 1e). The second was composed of the fundamental frequency and the first harmonic (Fo+H1, Fig. 1f). The third consisted of the fundamental frequency only (Fo, Fig. 1g).

(3) To test whether the distribution of energy in the spectrum is an important parameter for the pup's recognition of the mother, we performed selective digital filtration on natural calls (FFT window size: 2048, precision in frequency=10.8 Hz). Two signals were built: one with every third harmonic filtered (1H/3, Fig. 1h), and a second with every second harmonic filtered (1H/2, Fig. 1i).

(4) To assess the accuracy of pups' pitch discrimination, we performed positive and negative linear shifts (N=12). This was done by picking a data record through a square window, applying short-term overlapping (50%) Fast Fourier transform (FFT), followed by a linear shift (+ or −) of each spectrum, and by a short-term inverse Fast Fourier transform (FFT^{-1}, Randall & Tech 1987). The window size was 4096 points (ΔF=5 Hz). The values were +10, +50, +100, +200 (Fig. 1d), +250, +300, − 10, − 50, − 100, − 200 and − 250 Hz. In these experimental signals the natural amplitude and temporal structure (frequency and amplitude modulations) were unchanged.

Modifications in the temporal domain

(1) To test the importance of amplitude and frequency modulation in the individual recognition process, we prepared two experimental signals in which the temporal frequency pattern, or the temporal amplitude pattern, was modified. The first experimental signal had no amplitude modulation but had a natural frequency modulation (Fig. 2b). To build this signal, we used the analytical signal concept, which allows demodulation of amplitude using a Hilbert transformation (Seggie 1987). In the second experimental signal, the temporal frequency pattern was time reversed while all other parameters remained unchanged (Fig. 2c).

(2) To assess the minimal duration of a female's call necessary to elicit a pup's recognition of its mother, we prepared four signals: three corresponded to the first 25, 20 and 10% of the natural call (Fig. 2d, f, g, respectively), that is, containing entirely or partly the ascending frequency modulation, and the fourth consisted of the last 25% of the natural call (Fig. 2e), that is, contained entirely the descending frequency modulation. The mean duration of the signals was 143–375 ms (N=20).

RESULTS

Modifications in the Frequency Domain

Results are reported in Table 1.

(1) Both low- and high-pass signals elicited strong recognition of the mother's call by pups. However, the high-pass signal seemed to be less relevant than the low-pass one, since with the high-pass signal two of 11 pups were not able to recognize their mother's calls.

(2) Responses to the signal containing the fundamental frequency alone (Fo) and the control signal differed significantly, whereas both signals Fo+H1 and Fo+H1+H2 elicited a majority of positive responses.

(3) Responses to signals showing filtrations of one of two (1H/2) and one of three (1H/3) harmonics were much less strong than to those with the control signal.

(4) Most of the negative frequency-shifted signals did not trigger recognition of the mother's call. Only the − 10 and − 50 Hz signals elicited a positive response. In contrast, of the positive frequency-shifted signals, only the +300 Hz signal was not recognized by the pups. The +10, +50 and +100 Hz linear shifts elicited similar pup responses to those elicited by the control signal. The response to +200 and +250 signals was less strong, as a number of pups did not respond to these signals.

Modifications in the Temporal Domain

Results are reported in Table 2.

(1) There was a significant difference between the responses to the reversed FM signals and those elicited by the control signals: more than 50% of pups did not recognize their mother's calls with reversed FM. In

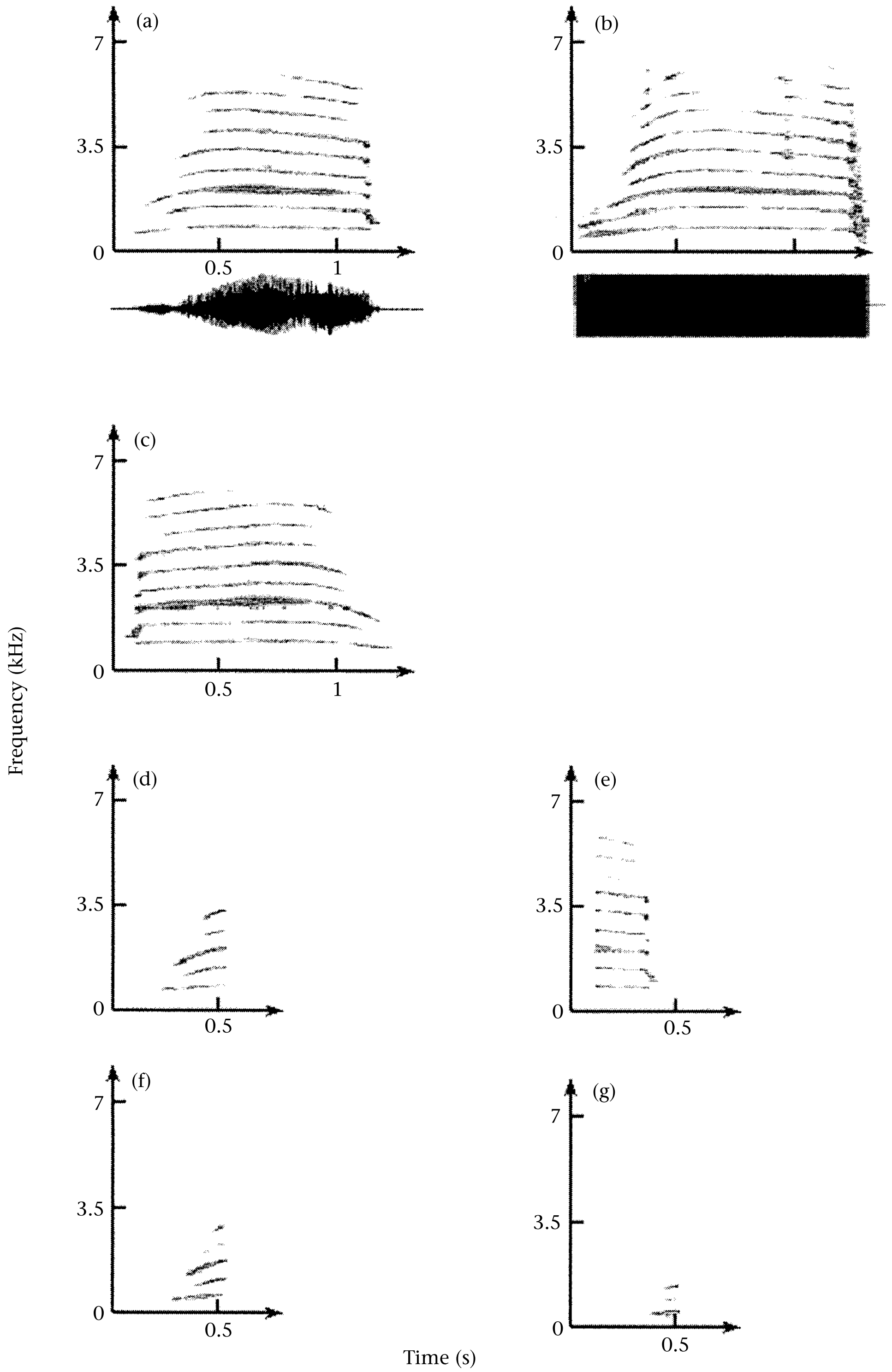

Figure 2. Spectrograms of a female's call modified in the temporal domain as used in playback experiments to pups. (a) Control, (b) without amplitude modulation (AM), (c) with time-reversed frequency modulation (FM), (d) first 25% of the natural signal, (e) last 25% of the natural signal, (f) first 20% of the natural signal, (g) first 10% of the natural signal. The oscillograms for (a) and (b) are added to illustrate the difference between signals (presence, in the control, or absence of amplitude modulation).

contrast, signals without amplitude modulation induced a majority of positive responses.

(2) Recognition did not occur when only the last 25% of the signal was present. In contrast, the presence of only the first 25% of the natural signal was sufficient to elicit a positive response from the pup. When only the first 20% or 10% remained, recognition was impaired.

Table 1. Response of fur seal pups to playback of the mother's call with modified frequency parameters

	Response†					
Experiments	0	1	2	*N*	*T*	*n*
Filtrations						
Low pass	0	8	3	11	2.0	3
Control	0	7	4			
High pass	2	7	2	11	2.5	5
Control	0	7	4			
Fo+H1+H2	0	6	1	7	2.5	2
Control	0	4	3			
Fo+H1	4	8	1	13	3.0	7
Control	0	9	4			
Fo	9	3	0	12	0.0**	10
Control	0	8	4			
1H/3	8	5	4	17	0.0**	8
Control	0	11	6			
1H/2	13	3	0	16	0.0**	16
Control	0	10	6			
Linear shift (Hz)						
+10	0	4	2	6	0.0	2
Control	0	4	2			
+50	0	3	3	6	2.0	3
Control	0	4	2			
+100	0	6	3	9	6.0	5
Control	0	5	4			
+200	2	4	3	9	6.0	7
Control	0	4	5			
+250	4	2	3	9	2.0	5
Control	0	5	4			
>+300	10	0	0	10	0.0**	10
Control	0	5	5			
−10	0	7	2	9	0.0	1
Control	0	7	2			
−50	0	8	1	9	0.0	1
Control	0	7	2			
−100	4	4	1	9	0.0*	5
Control	0	7	2			
−200	5	3	1	9	0.0*	6
Control	0	7	2			
−250	7	0	0	7	0.0*	7
Control	0	6	1			

N: number of pups tested; *n*: number of non-null differences between the control and experimental signal, tested with Wilcoxon signed-ranks test: **P*<0.05; ***P*<0.01.

†0=no reaction; 1=reaction during playback; 2=reaction during and after playback.

Table 2. Response of fur seal pups to playback of the mother's call with modified temporal parameters

	Response†					
Experiments	0	1	2	*N*	*T*	*n*
Modulation						
Without AM	2	6	1	9	2.5	6
Control	0	4	5			
With reversed FM	7	5	1	13	0.0**	10
Control	0	4	9			
Call duration						
First 25%	1	5	10	16	9.0	6
Control	0	8	8			
First 20%	8	8	3	19	4.5*	11
Control	0	12	7			
First 10%	14	2	1	17	6.5**	17
Control	0	10	7			
Last 25%	15	0	0	15	0.0**	15
Control	0	8	7			

N: number of pups tested; *n*=number of non-null differences between the control and experimental signal, tested with Wilcoxon signed-ranks test: **P*<0.05; ***P*<0.01.

†0=no reaction; 1=reaction during playback; 2=reaction during and after playback.

DISCUSSION

Acoustic Parameters used in Identification

To our knowledge, few experimental studies have investigated which acoustic parameters are used in the mother–pup recognition process in mammals. Although the occurrence of mother–offspring recognition has been reported, or experimentally shown, in some mammal species, and in some cases the acoustic signature described, no one has shown which acoustic features are involved in the individual identification process (e.g. sheep, *Ovis aries*, goat, *Capra hircus*: Shillito & Alexander 1975; Gubernick et al. 1979; Addae et al. 2000; Ferreira et al. 2000; northern fur seal: Bartholomew 1959; Insley 1992; elephant seal, *Mirounga angustirostris*: Petrinovich 1974; galapagos fur seal and sealion, *Zalophus californianus wollebacki*: Trillmich 1981; subantarctic fur seal: Charrier et al., 2003; rhesus monkey, *Macaca mulatta*: Rendall et al. 1996; dolphin, *Tursiops truncatus*: Sayigh et al. 1999).

In our study, the recognition process appeared to rely on several cues in the frequency and temporal domains. This is relevant to previous studies on birds which showed that birds use a multiparametric analysis to recognize each other (great tits, *Parus major*: Weary 1990; penguins: Jouventin et al. 1999; Aubin & Jouventin 2002; gulls: Charrier et al. 2001a). In the frequency domain, the whole frequency spectrum was not required for recognition to occur. Each part of the spectrum, both low and high, was able to support the pup's recognition of the mother, although the experimental signal containing only the high part of the spectrum seemed less efficient than that with only the low part. However, although the whole bandwidth was not required for recognition, pups paid great attention to the harmonic structure of the female's call. Disruption of the energy distribution strongly impaired identification: when one of two or three harmonics was removed, most of the pups failed to recognize their mother's calls. Furthermore, signals containing only one or no harmonics did not allow recognition. In the frequency domain, the properties of the energy spectrum appeared to be the key component supporting recognition of the mother's call by the pup.

Experiments with the shifted signals showed that pups took into account the absolute values of frequencies, for example a linear shift of +200 Hz weakly impaired recognition. A surprising result was that pups were more sensitive to negative than positive linear shift: pups did not recognize their mother's calls with a shift of

− 100 Hz. In the king penguin, *Aptenodytes patagonicus*, similar experiments have given opposite results: chicks were more sensitive to the effect of positive than negative shifting of frequency (Jouventin et al. 1999). In the black-headed gull, *Larus ridibundus*, chicks were extremely sensitive to positive frequency shifts as well as to negative ones (Charrier et al. 2001a). No hypothesis has been put forward to explain these differences.

In the temporal domain, amplitude modulation was not essential for recognition. Similarly, this acoustic feature is not involved in individual recognition in colonial species of birds (Jouventin et al. 1999; Charrier et al. 2001a; Aubin & Jouventin 2002). Such a parameter would not be reliable: propagation experiments have shown that amplitude modulation is subject to strong distortion during transmission in a noisy environment (Wiley & Richards 1978). However, amplitude modulations might be important in the localization of the caller (Saberi et al. 1999).

In contrast, recognition was impaired when the frequency modulation was modified: more than half of pups were not able to recognize their mother's calls with a time-reversed frequency modulation. Furthermore, 15 of 16 pups were able to recognize modified mother's calls reduced to the first quarter of the call whereas no recognition occurred when only the last quarter of the call remained. Thus, pups seemed to pay particular attention to the ascending frequency modulation at the beginning of the call. In contrast, they did not use the descending frequency modulation at the end of the female's call. The first quarter of the call (mean duration 375 ms) containing the ascending frequency modulation must therefore support sufficient information to allow pups to recognize their mother's call unambiguously. This result is not surprising since an analysis using frequency modulations seems to be the most effective for detecting a signal in a noisy environment (Lee 1960; Okanoya & Dooling 1991). It is striking that colonial birds confronted with such harsh environmental constraints also use frequency modulation for parent–offspring, or between–mates, recognition (Charrier et al. 2001a; Aubin & Jouventin 2002).

Recognition by Pups and Females

In a previous study (Charrier et al. 2002a), we showed that fur seal females recognize the calls of their pup, and that this recognition relies on a multiparametric analysis of the vocal individual signature of each pup's calls. The main parameter used by females is the characteristic of the call frequency modulation: all females failed to identify their pup's call if it had been experimentally time reversed (Charrier et al. 2002a). Here, we have shown that more than 50% of pups did not react to a time-reversed mother's call. Thus, it appears that frequency modulation of calls is a key factor in recognition for both mothers and pups but pups showed a high tolerance to modifications of this parameter whereas females seemed to be especially sensitive to them.

In contrast, pups paid particular attention to the distribution of energy among harmonics whereas females could recognize their pup's calls in spite of disruption of this parameter. An experimental signal in which every second harmonic had been removed impaired recognition in 82% of pups, whereas 62% of females still responded (Charrier et al. 2002a). When only every third harmonic was removed, 47% of pups still failed to recognize the modified signal whereas more than 80% of females recognized their pup's calls (Charrier et al. 2002a). Thus, fur seal pups seem to be more sensitive to the energy spectrum than females.

To summarize, the mutual recognition process is asymmetrical with regard to the perceptual basis developed by mother and pup: pups seem to use mainly a spectral analysis of the signal to identify their mother's call, and females seem to rely mainly on a temporal analysis of the signal to recognize their pup's calls. From a proximal point of view, we hypothesize that this perceptual difference could be linked to the degree of maturity of the central nervous system. From an evolutionary point of view, one could ask if this asymmetry in recognition may be explained by differences in the ecological constraints on mother and pup. In fur seal colonies, there is a loud background noise which masks the calls of both mothers and pups. Furthermore, because of the high density of fur seals there is a risk of confusion between individuals. When a mother comes back from a foraging trip, she is confronted with both acoustic jamming and a high risk of visual confusion, and finding her pup under such conditions seems to be difficult. Some acoustic parameters are better adapted to support communication in a noisy environment. Frequency modulation, which is not modified during propagation, appears to be a reliable cue for recognition in a noisy channel. In contrast, the energy spectrum is more likely to be modified during its propagation as high-pitched frequencies are rapidly attenuated (Wiley & Richards 1978). By primarily using frequency modulation to identify their pup's calls, fur seal females use the more reliable acoustic parameter over long range, allowing them to assess the presence of their pup among several others even when calling from a great distance. This may be essential because, when the mother comes back from the sea, she does not know where her pup is within the colony. Pups may be less effective in this long-range recognition process.

Acknowledgments

We thank the members of the 50th and the 51st scientific missions to Amsterdam Island for their help in the field and particularly Gwenaël Beauplet, Murielle Ghestem, Rémy Andrada, Catherine Baur, Yann François, Arnaud Jeulin, Florence Patural, Sébastien Ricaud and Vincent Rouvreau. This research was supported in the field by the 'Institut Polaire Français Paul-Emile Victor (IPEV)'. I.C. was supported financially by the Ministère de l'Education Nationale, de Recherche et de la Technologie (MENRT). Many thanks to Dr Peter Bowden who improved the English. We are grateful to Dr Thierry Aubin, Dr Sofie Van Parijs and an anonymous referee for their kind and numerous comments.

References

Addae, P. C., Awotwi, E. K., Oppong-Anane, K. & Oddoye, E. O. K. 2000. Behavioural interactions between West African dwarf nanny goats and their single-born kids during the first 48 hours post-partum. *Applied Animal Behavioural Science*, **65,** 53–61.

Aubin, T. 1994. Syntana: a software for the synthesis and analysis of animal sounds. *Bioacoustics*, **6,** 80–81.

Aubin, T. & Jouventin, P. 2002. How to vocally identify kin in a crowd: the penguin model. *Advances in the Study of Behaviour*, **31,** 243–277.

Bartholomew, G. A. 1959. Mother-young relations and the maturation of pup behaviour in the Alaska fur seal. *Animal Behaviour*, **7,** 163–171.

Beecher, M. D., Beecher, I. M. & Hahn, S. 1981. Parent-offspring recognition in bank swallows (*Riparia riparia*): II. Development and acoustic basis. *Animal Behaviour*, **29,** 95–101.

Boness, D. J. 1990. Fostering behavior in Hawaiian monk seals: is there a reproductive cost? *Behavioral Ecology and Sociobiology*, **27,** 113–122.

Charrier, I., Mathevon, N., Aubin T. & Jouventin, P. 2001a. Acoustic communication in a black-headed gull colony: how chicks identify their parents? *Ethology*, **107,** 961–974.

Charrier, I., Mathevon, N. & Jouventin, P. 2001b. Mother's voice recognition in seal pups. *Nature*, **412,** 873.

Charrier, I., Mathevon, N. & Jouventin, P. 2002a. How does a fur seal mother recognize the voice of her pup? An experimental study of *Arctocephalus tropicalis*. *Journal of Experimental Biology*, **205,** 613–622.

Charrier, I., Mathevon, N., Hassnaoui, M., Carraro, L. & Jouventin, P. 2002b. The subantarctic fur seal pup switches its begging behaviour during maternal absence. *Canadian Journal of Zoology*, **80,** 1250–1255.

Charrier, I., Mathevon, N. & Jouventin, P. 2003. Individuality in the voice of fur seal females: an analysis study of the Pup Attraction Call in *Arctocephalus tropicalis*. *Marine Mammal Science*, **19,** 161–172.

Ferreira, G., Terrazas, A., Poindron, P., Nowak, R., Orgeur, P. & Levy, F. 2000. Learning of olfactory cues is not necessary for early lamb recognition by the mother. *Physiology and Behavior*, **69,** 405–412.

Georges, J. Y. & Guinet, C. 2000. Maternal care in the subantarctic fur seals on Amsterdam island. *Ecology*, **81,** 295–308.

Georges, J. Y., Sevot, X. & Guinet, C. 1999. Fostering in a subantarctic fur seal. *Mammalia*, **63,** 384–388.

Gubernick, D. J., Jones, K. C. & Klopfer, P. H. 1979. Maternal 'imprinting' in goats. *Animal Behaviour*, **27,** 314–315.

Halliday, T. 1983. Information and communication. In: *Animal Behaviour Communication. Vol. 2* (Ed. by T. R. Halliday & P. J. B. Slater), pp. 43–81. Oxford: Blackwell Scientific.

Insley, S. J. 1992. Mother-offspring separation and acoustic stereotypy: a comparison of call morphology in two species of pinnipeds. *Behaviour*, **120,** 103–121.

Insley, S. J. 2000. Long-term vocal recognition in the northern fur seal. *Nature*, **406,** 404–405.

Insley, S. J. 2001. Mother-offspring vocal recognition in northern fur seals is mutual but asymmetrical. *Animal Behaviour*, **61,** 129–137.

Jouventin, P., Aubin, T. & Lengagne, T. 1999. Finding a parent in a king penguin colony: the acoustic system of individual recognition. *Animal Behaviour*, **57,** 1175–1183.

Lee, Y. M. 1960. *Statistical Theory of Communication*. New York: J. Wiley.

Lengagne, T., Aubin, T., Jouventin, P. & Lauga, J. 2000. Perceptual salience of individually distinctive features in the calls of adult king penguins. *Journal of the Acoustical Society of America*, **107,** 508–516.

McArthur, P. 1982. Mechanisms and development of parent-young vocal recognition in the piñon jay. *Animal Behaviour*, **30,** 62–74.

McGregor, P. K., Catchpole, C. K., Dabelsteen, T., Falls, J. B., Fusani, L., Gerhard, C., Gilbert, F., Horn, A. G., Klump, G. M., Kroodsma, D. E., Lambrechts, M. M., McComb, K. E., Nelson, D. A., Pepperberg, I. M., Ratcliffe, L., Searcy, W. A. & Weary, D. M. 1992. Design of playback experiments: the Thornbridge Hall NATO ARW consensus. In: *Playback and Studies of Animal Communication* (Ed. by P. K. McGregor), pp. 1–9. New York: Plenum.

Okanoya, K. & Dooling, R. J. 1991. Detection of species-specific calls in noise by zebra finches *Poephila guttata* and budgerigars *Melopsittacus undulatus*: time or frequency domain? *Bioacoustics*, **3,** 163–172.

Paulian, P. 1964. Contribution à l'étude de l'otarie de l'île d'Amsterdam. *Mammalia*, **28,** 1–146.

Petrinovich, L. 1974. Individual recognition of pup vocalisation by northern elephant seal mothers. *Zeitung Tierpsychologie*, **34,** 308–312.

Randall, R. B. & Tech, B. 1987. *Frequency Analysis*. Naerum: Brüel & Kjaer.

Rendall, D., Rodman, P. S. & Emond, R. E. 1996. Vocal recognition of individuals and kin in free-ranging rhesus monkeys. *Animal Behaviour*, **51,** 1007–1015.

Riedman, M. 1990. *The Pinnipeds: Seals, Sea Lions and Walruses*. Los Angeles: University of California Press.

Saberi, K., Takahashi, Y., Farahbod, H. & Konishi, M. 1999. Neural bases of an auditory illusion and its elimination in owls. *Nature Neuroscience*, **2,** 581.

Sayigh, L. S., Tyack, P. L., Wells, R. S., Scott, M. D. & Irvine, A. B. 1999. Individual recognition in wild bottlenose dolphins: a field test using playback experiments. *Animal Behaviour*, **57,** 41–50.

Seggie, D. 1987. The application of analytic signal analysis in speech processing. *Processing Institute of Acoustics*, **8,** 82–85.

Shillito, E. & Alexander, G. 1975. Mutual recognition amongst ewes and lambs of four breeds of sheep (*Ovis aries*). *Applied Animal Ethology*, **1,** 151–165.

Sokal, R. R. & Rohlf, F. J. 1995. *Biometry*, 3rd edn. New York: W. H. Freeman.

Trillmich, F. 1981. Mutual mother-pup recognition in Galapagos fur seals and sea lions: cues used and functional significance. *Behaviour*, **78,** 21–42.

Trivers, R. L. 1974. Parent-offspring conflict. *American Zoologist*, **14,** 249–264.

Weary, D. M. 1990. Categorization of song notes in great tits: which acoustic features are used and why? *Animal Behaviour*, **39,** 450–457.

Wiley, R. H. & Richards, D. G. 1978. Physical constraints on acoustic communication in the atmosphere: implication for the evolution of animal vocalizations. *Behavioral Ecology and Sociobiology*, **3,** 69–94.