Finding a parent in a king penguin colony: the acoustic system of individual recognition

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To be fed, a king penguin, *Aptenodytes patagonicus*, chick must identify the call of its parents, in the continuous background noise of the colony. To study this recognition process, we played back to the chicks parental calls with acoustic parameters modified in the temporal and frequency domains. The parental call is composed of syllables (complex sounds with harmonic series) separated by pronounced amplitude declines. Our experiments with modified signals indicate that the chick's frequency analysis of the call is not tuned towards precise peak energy values, the signal being recognized even when the carrier frequency was shifted 100 Hz down or 75 Hz up. To recognize the adult, chicks used frequency rather than amplitude modulation, in particular the frequency modulation shape of the syllable. This structure is repeated through the different syllables of the call giving a distinct vocal signature. Our experiments also show that the receiver needs to perceive only a small part of the signal: the first half of the syllable (0.23 s) and the first three harmonics were sufficient to elicit recognition. The small amount of information necessary to understand the message, the high redundancy in the time and frequency domains and the almost infinite possibilities of coding provided by the frequency modulation signature permit the chick to recognize the adult, without the help of a nest site. For these reasons, the code used in the call of the king penguin can be regarded as a functional code, increasing the possibility of individual recognition in an acoustically constraining environment.

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In birds, many vocal exchanges, particularly between mates and between parents and young, occur at short range, over distances of a few metres at most (Falls 1982). At these short distances, the signal is only weakly modified during propagation, by, for example, the ground effect, atmospheric absorption or geometric attenuation (Wiley & Richards 1978; Dabelsteen 1984; Dabelsteen et al. 1993). Nevertheless, even at short range, communication between individuals may sometimes be difficult, for example in noisy environments, such as dense colonies of birds. In these colonies, a continuous background noise is generated by sounds used for communication and by other sounds such as wind, waves, beak clapping and wing flapping. The level of ambient noise is high (more than 70 dB: Robisson 1991; Mathevon 1996) and consequently the value of the signal-to-noise ratio is low. In addition, the numerous vocalizations generate jamming in both frequency and temporal domains. Thus,

it is difficult for individuals in the colony to extract information from the background noise.

Seabird colonies are particularly crowded and noisy. Breeding on land and feeding at sea, mates are separated for days or weeks during the breeding season, but are faithful to each other and to their offspring (see Jouventin 1982 for penguins). The ability to recognize mates, parents or chicks is particularly important in seabird colonies, where nest sites are densely packed, increasing the possibility of confusion (Hutchison et al. 1968). To find the egg(s) or chick(s), nesting birds also use landmarks, so to isolate vocal recognition in this study, we used a non-nesting species, the king penguin, *Aptenodytes patagonicus*.

King penguins breed on flat areas in homogeneous and dense monospecific colonies numbering thousands of birds (1.6 breeders/m²; Guinet et al. 1995). There are no nest sites: each bird carries its egg and then its small chick on its feet. At the end of the breeding cycle, as in our study, each individual is identified by its chick only by vocal cues (the 'long call' in the behavioural repertoire described by Stonehouse 1960) and a few landmarks (Derenne et al. 1979 for the king penguin; Jouventin

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1982 for the penguin family). Observations of banded birds and playback experiments show that only the mate responds to its partner coming back. Similarly, chicks respond only to their parents (or their calls played back). For the chick, recognition of the parental call is important for survival as parents usually only feed a chick they have identified by its call (Jouventin 1982). Nevertheless, some adoptions do occur (Stonehouse 1960) by failed breeders (Jouventin & Mauget 1996).

That birds can recognize one another by voice alone has been demonstrated repeatedly. In numerous studies (for reviews see Falls 1982; Dhondt & Lambrechts 1992), the structure of the signal has been analysed, to determine which parameters encode acoustic identity and allow recognition between individuals. An ideal signal for individual recognition would be highly stereotyped within each individual but would differ noticeably between individuals. A method of quantifying this is to define a ratio of acoustic parameters such as Cvb/Cvi, where Cvb is the coefficient of variation between individuals and Cvi the coefficient of variation within individuals (Hutchison et al. 1968; for a review see Scherrer 1984). The Cvb/Cvi ratio and coefficients of correlation have been calculated for the king penguin call (Jouventin 1982; Robisson 1992; Lengagne et al. 1997): the between-individual variation was less stereotyped and on average three times greater than the within-individual variation for time parameters and four times greater for frequency parameters. Thus, individuals encode their call by making it highly stereotyped.

Knowing that it is possible to distinguish the signals of individuals statistically does not, however, tell us how birds manage do it. Playback experiments are needed to investigate this. Our previous observations (Jouventin 1982) and experiments (Aubin & Jouventin 1998) show that king penguin chicks are able to decode a precise acoustic signal despite extreme jamming and high-level background noise generated by the colony (called the 'cocktail-party effect' in humans by Cherry 1966), suggesting that a variety of fine details are fitted into the code. How can penguins appreciate subtle qualities of sounds in such a noisy and jamming environment? How can acoustic individuality be encoded when faced by such strong acoustical constraints?

Detection of signals in noise is a complex issue. The most detailed knowledge of the mechanisms involved comes from psychoacoustic experiments performed in controlled laboratory environments (Klump 1996). Few field studies have studied experimentally how signals of animals are detected amidst background noise in the natural environment. The capacity of the king penguin chick to recognize the parental call requires peculiar strategies of coding/decoding. Our aim in this study was to determine to which acoustic parameters the chick is tuned in order to extract the information from the background noise. For this purpose, we broadcast different parental calls modified in the frequency and temporal domains, to chicks waiting in the colony for their parents to return from the sea.

METHODS

Subjects and Location

We studied king penguins at Ile Possession, Crozet archipelago (46°25′S, 51°45′E) from early December 1995 to mid-January 1996. The study was conducted at Baie du Marin, in a large colony containing about 40 000 pairs of adults and 1500 chicks. The chicks we tested were between 10 and 12 months old. At this stage of its life, the chick is pushed away by new breeders from where the egg was laid but is entirely dependent on its parents for food. To identify them, we banded tested chicks on a flipper with a temporary plastic band.

Recording Procedure

To record parental calls of king penguins (the 'long call' of Stonehouse 1960) we used an omnidirectional Sennheiser MD211 microphone (frequency response 150–18 000 Hz ± 1 dB) mounted on a 2.5-m perch and connected to a Sony TCD10 Pro II digital audiotape recorder (sampling frequency: 44.6 kHz, frequency response flat within the range 20–20 000 Hz ± 1 dB). The distance between the beak of the recorded bird and the microphone was approximately 1 m.

Sound Synthesis and Analysis

Signals were digitized with a 16-bit Oros Au21 acquisition card (with a 120-dB/octave antialiasing filter) at a sampling frequency of 16 kHz and stored on the hard disk of a PC computer. They were then examined and modified with the Syntana analytical package (Aubin 1994). Sound pressure level measurements (SPL in dB) were measured with a Bruël & Kjaer Sound Level Meter type 2235 (linear scale, slow setting) equipped with a 1-inch condenser microphone type 4176.

Playback Procedure

For playback experiments we used a 4200 Uher tape-recorder (tape speed 19 cm/s) connected to a 50-W Audix PH3 self-powered loudspeaker (frequency response 100–5600 Hz ± 2 dB). Signals were played at a natural sound pressure level (Robisson 1993a), of approximately 95 dB, measured 1 m from the loudspeaker.

We conducted tests between 1000 and 1700 hours, during clear and dry weather, with a wind speed of less than 4 m/s. The chick was generally resting in the feeding area, preening itself. The distance between the loud-speaker and the bird was ca. 7 m, this corresponding to a natural calling distance of an adult (Robisson 1993b). At first, chicks were tested with the natural call of one of their parents. A few chicks (1/20) that did not respond because they had just been fed were tested the next day. Only chicks whose intensity of response was ranked 4 (see criteria of responses below) were kept for further tests with modified signals. Thus, the population of chicks tested was homogeneous in motivation to detect the

parental call. All these chicks reacted without ambiguity. To minimize habituation, we tested chicks with the experimental signals 2 or 3 days after testing them with a natural call, while their parents were absent. We broadcast two identical experimental signals, separated by an interval of 5 s, to a chick in a feeding area with a normal density of birds; then 15 min later, we broadcast another series of two identical signals. The 15-min period between broadcasts allowed the chick to recover its natural activity. To prevent habituation, a maximum of three series of signals a day was broadcast to any one chick. Each chick was tested with all the different types of signal. The order of presentation of the signals was randomized for the different chicks tested. In the same way, the order of presentation of experimental signals from day to day was not the same for each chick. Hence, the observed responses for the whole group of chicks tested were neither a result of cumulative excitation nor dependent on playback order. To avoid a possible masking effect not studied here (see Aubin & Jouventin 1998), experimental signals were broadcast only during relative periods of silence, that is, when birds in the vicinity of the tested chick remained silent.

Criteria of Responses

In natural conditions, when the parents are absent, the chick remains silent, lying quietly. The adult, returning from the sea to feed its chick, makes its way to the area of the colony where the chick is usually located (rendezvous site) and calls at regular intervals. The chick in the flock holds up its head, calls in reply and moves towards the parent, often running (Stonehouse 1960; Jouventin 1982). The other chicks in the vicinity, resting or preening themselves, never react to the extraneous calls and their behaviour does not change.

To evaluate the intensity of response of tested chicks to playback signals, we used a five-point scale, as follows: 0 (none): no reaction; 1 (weak): head turning, agitation; 2 (medium): head turning and calls after the second broadcast; 3 (strong): head turning, calls after the first broadcast; and 4 (very strong): head turning, calls after the first broadcast, approaches in the direction of the loudspeaker and stops in the vicinity (less than 3 m). This behavioural scale is similar to those used in previous studies on the king penguin (see Derenne et al. 1979; Jouventin et al. 1979; Robisson 1990).

Statistical Analysis

Statistics and interpretations of results were based on the analysis of the distribution of the observed values within the five response classes. To compare paired samples in more than two categories, we used the marginal homogeneity test (Agresti 1990) together with exact two-sided P values. When the same marginal distribution was used through several comparisons, we used the Bonferroni-corrected P values to assess the final significance of the test. Computations of exact two-sided P values were carried out with StatXact software (Cytel 1995). We used a significance level of $P \leq 0.05$.

Experimental Signals

We tested 17 experimental signals. These consisted of natural calls modified in the frequency and temporal domains.

The original signal

This signal was the natural parental call specific to the chick being tested. So, for each chick tested there was an original signal corresponding to the call of one of the parents (male or female) and a series of experimental signals. Figures 1 and 2 show an example of a natural parental call. The call corresponds to a series of sound components, termed syllables by Jouventin (1982), separated by strong amplitude declines which coincide with falls in frequency. The call duration varied from 3 to 6 s ($\bar{X} \pm SD = 4.45 \pm 1.16$ s, $N = 66$), the first syllable generally being the longest. The spectral composition of syllables corresponds to harmonic series. Most of the energy is concentrated between 500 and 2500 Hz, with a maximum level corresponding most often to the harmonic (twice the fundamental frequency, F_o).

Signals with a modified harmonic structure

We modified the parental calls in two ways.

(1) The parental call was filtered by low-pass or high-pass digital filters (Fig. 1) by applying optimal filtering with a fast Fourier transform (FFT; Press et al. 1988; Mbu-Nyamsi et al. 1994). The window size of the FFT was 4096 Hz (precision in frequency: $\Delta F = 4$ Hz). Four signals were constructed (Fig. 1): with the fundamental frequency alone; with the fundamental (F_o) and the first harmonic ($2F_o$); with the lower part of the spectrum ($F_o + 2F_o + 3F_o$); and with the upper part of the spectrum (between 2000 and 8000 Hz).

(2) The parental call was shifted up or down in frequency. This was done by picking a data record through a square window, applying short-term overlapping (50%) 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 Hz ($\Delta F = 4$ Hz). The linear shifts of the spectra were +100, +75, +50, −50, −75 and −100 Hz. These values were chosen on the basis of the natural distribution of fundamental frequency values. Except for these modifications of the pitch of the carrier frequency, temporal and amplitude parameters of the parental call were unchanged.

Signals with a modified temporal pattern

We modified both frequency and amplitude modulations (FM and AM) and the syllable duration of natural calls.

(1) For FM and AM modifications, two signals were constructed. (a) A natural AM was applied to a carrier frequency without FM (Fig. 2). The carrier frequency was a harmonic series and the value of the fundamental corresponded to the mean value of the fundamental frequency of the parental call. We applied to this carrier
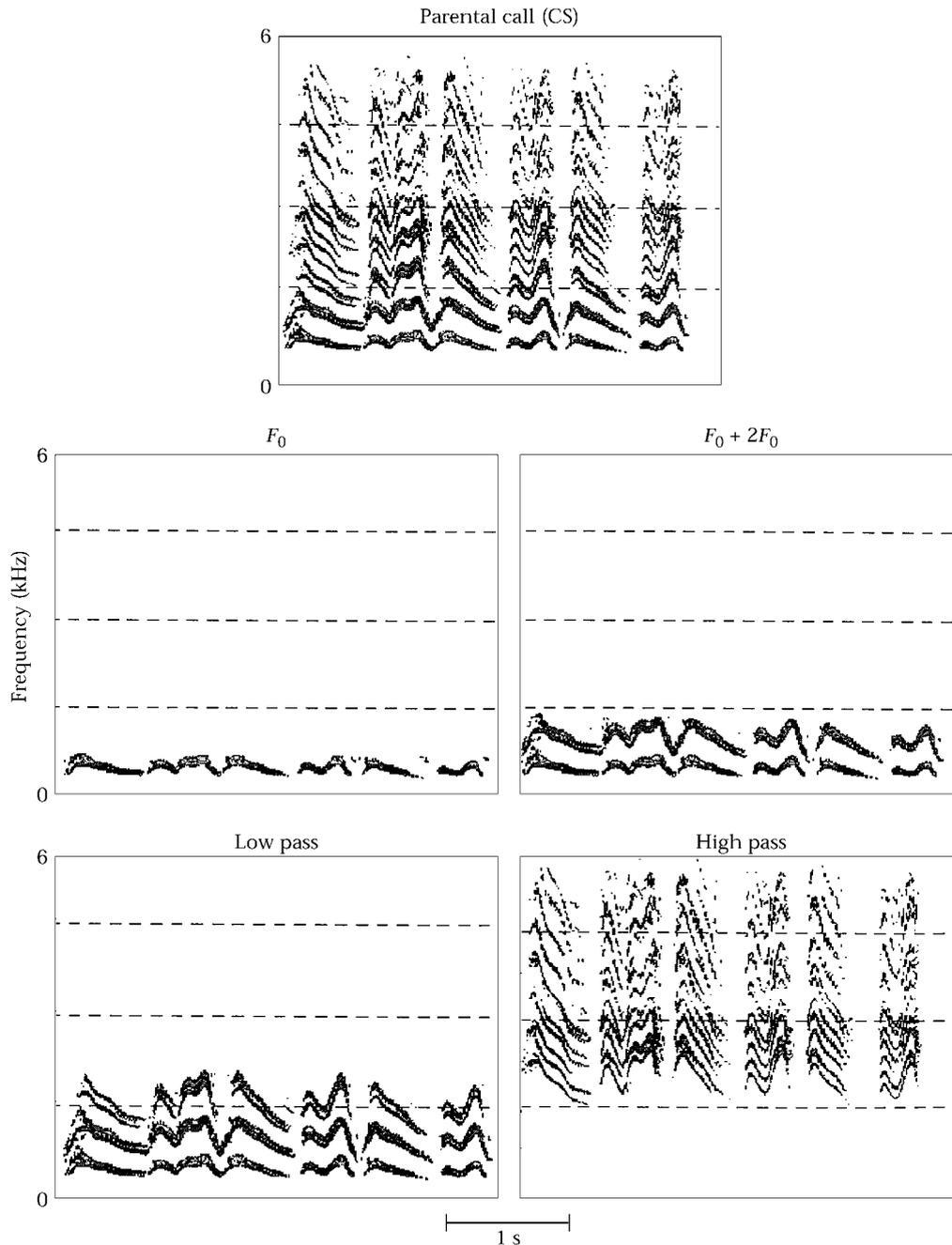
Figure 1. Sound spectrograms of a king penguin parental call and of the four experimental signals corresponding to the same call modified in the frequency domain.

frequency the natural AM (the envelope) that was extracted from the call of the parent, using the Hilbert transform calculation (Seggie 1987; Brémond & Aubin 1992; Mbu-Nyamsi et al. 1994). In these conditions, because of the application of the envelope, the temporal succession of syllables of the parental call was maintained. The only difference between this call and the natural call was the lack of FM. (b) The AM of the parental call was removed without modification of the natural FM and the natural carrier frequency. To do this, we used analytical signal analysis (Mbu-Nyamsi et al. 1994). The

result was a signal with a normal FM and duration, but without any AM.

(2) To modify syllable duration, we truncated the syllable. To prevent spectral artefacts arising from an abrupt gap in amplitude, an envelope was applied (by multiplication) to the data set in the time domain so as to smooth all the edges. As previously, the Hilbert transform calculation was used to build the envelope. Previous studies (Derenne et al. 1979; Jouventin 1982) have shown that the broadcast of a part of the parental call is sufficient to elicit the chick's response. In the present study, we
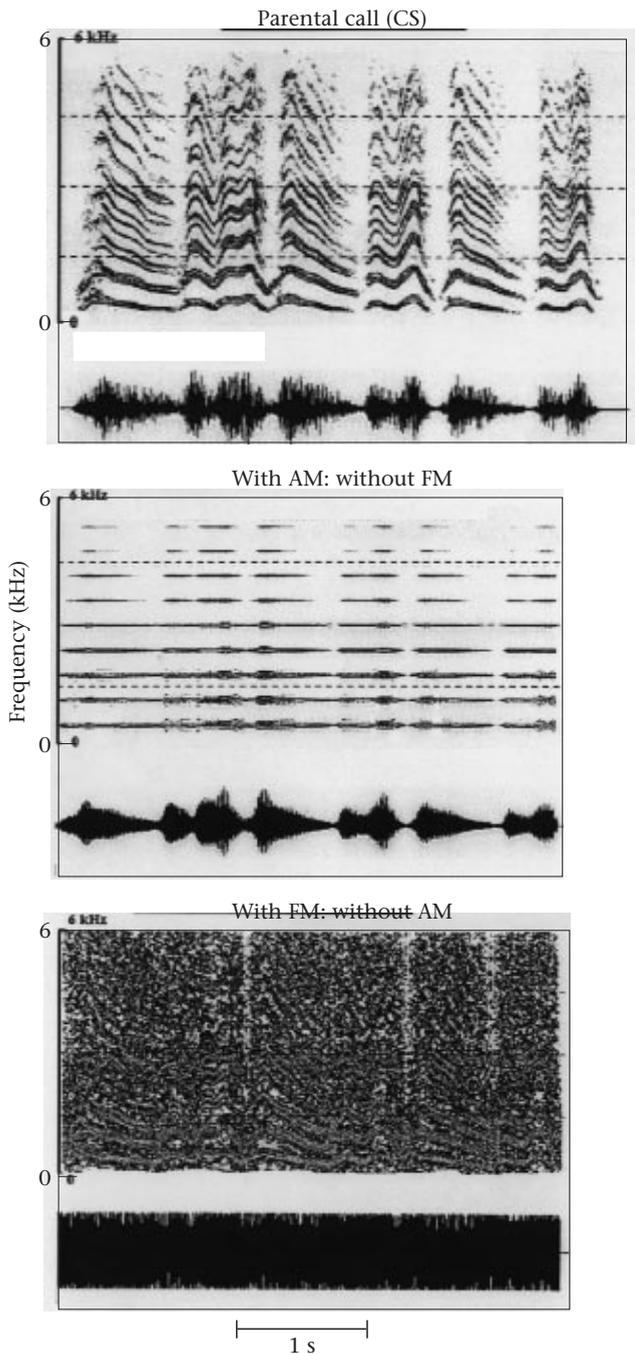
Figure 2. Sound spectrograms of the parental call shown in Fig. 1 and of the two experimental signals corresponding to the same call but with either the amplitude modulation (AM) or the frequency modulation (FM) removed.

broadcast signals where only the first or a part of the first syllable of the parental call was present. We constructed five signals: with the first syllable (Sy1); with a syllable belonging to the middle of the call (Sym); with the first half of the first syllable (H1Sy1); with the second half of the first syllable (H2Sy1); and with the first quarter of the first syllable (Q1Sy1). The mean duration $\pm$ SD of the syllables of the calls tested was 0.462 ± 0.011 s (N=17).

RESULTS

To simplify the results, we grouped response classes 0 and 1 together as negative responses, and classes 2, 3 and 4 as positive responses. Effectively, it was only for classes 2, 3 and 4 that recognition appeared clearly, with a call in reply to the signal broadcast. In contrast, for class 1 responses, chicks only looked towards the loudspeaker, not particularly because they recognized the parental call but more probably because they were surprised by an unusual (nonspecific?) signal. As a general rule, the chicks did not recognize the manipulated signals as well as they did the original parental call (Agresti's marginal homogeneity test: $P<0.05$).

Harmonic Structure

Table 1 shows the results. There was no significant difference between responses to F_o and to F_o+2F_o. For both signals a majority of positive responses was observed. In contrast, there was a significant difference between the low-pass and the high-pass signals, the latter eliciting a majority of negative responses.

There were significant differences between some frequency-shifted signals, but they elicited a majority of positive responses (Table 1) except for the +100-Hz signal, which differed significantly from all other signals (marginal homogeneity tests: +100 Hz versus: +75 Hz: S=25; +50 Hz: S=29; -50 Hz: S=29; -75 Hz: S=28; -100 Hz: S=18; $P<0.001$ in all cases except -100 Hz where P=0.005).

Temporal Pattern

Table 2 shows the results. Signals with a natural AM and without FM did not trigger a response. In every case (except one instance of head turning), chicks remained stationary, resting or preening themselves, as before the broadcast. In contrast, signals with a natural FM and without AM triggered recognition. These signals differed significantly.

The broadcast of one syllable was sufficient to elicit recognition (majority of positive responses). Recognition was not linked to a particular syllable since it was observed for both the first syllable and one from the middle of the call (no significant difference between Sy1 and Sym). The majority of chicks recognized just the first half of the first syllable (mean duration $\pm$ SD=0.231 ± 0.005 s, N=17; no significant difference between Sy1 and H1Sy1). Recognition did not occur when only the first quarter or the second half of the first syllable was broadcast (significant difference between Sy1 on the one hand and Q1Sy1 and H2Sy1 on the other).

DISCUSSION

Which Parameters Encode Acoustic Identity?

That the chicks did not recognize the manipulated signals as well as they did the original signal, that is, the

Table 1. Responses of king penguin chicks to parental calls with modified frequency parameters

	Responses						Marginal homogeneity tests	
Experiments	0	1	2	3	4	N	S	P
Filtration								
F_o	5	3	2	5	1	16	24	0.351
F_o+2F_o	2	0	1	6	3	12		
Low pass	0	0	0	8	8	16	62	0.0004
High pass	5	5	3	1	2	16		
Linear shift (Hz)								
+100	8	3	1	4	0	16	25	0.0002
+75	0	2	2	7	5	16	26	0.016
+50	0	0	0	6	10	16	8	1.000
−50	0	0	0	4	12	16	28	0.013
−75	1	1	1	6	7	16	56	0.039
−100	3	1	4	7	1	16		

For the linear shift series, P values are Bonferroni corrected.

Table 2. Responses of king penguin chicks to parental calls with modified temporal parameters

	Responses						Marginal homogeneity tests	
Experiments	0	1	2	3	4	N	S	P
Modulation								
Without FM	15	1	0	0	0	16	16	<0.001
Without AM	0	0	0	7	10	17		
Syllable duration								
1st syllable (Sy1)	1	2	1	11	2	17	29	3.375
Middle syllable (Sym)	1	1	2	4	2	12	19	0.750
1st half of 1st syllable (H1Sy1)	4	1	1	8	1	15	41	0.004
2nd half of 1st syllable (H2Sy1)	10	1	1	0	0	12	53	<0.001
1st quarter of 1st syllable (Q1Sy1)	12	1	1	0	0	14		

For the syllable duration series, P values are Bonferroni corrected.

parental call, is not surprising. The majority of birds use a complex of differentially weighted parameters, rather than any simple feature, to recognize their signals. This has been shown for songs (Weary 1990) and for calls (Gaioni & Evans 1986; Dooling et al. 1987). The king penguin is similar in this respect. Thus, the lack of some parameters even weakly important for individual recognition in our manipulated calls would explain the different level of response to the manipulated signal.

Our experiments on harmonic structure show that chicks pay attention to the low part of the spectrum of their parents' call, not to the higher part. Only the low-pass calls were recognized by the chicks. Even a signal with only the F_o and $2F_o$ retained was still recognized. Nevertheless, a parental call with only the fundamental frequency kept was not recognized. A pure tone, such as a signal with the fundamental alone, is therefore not sufficient and the addition of the first harmonic is necessary to trigger a response. Thus we conclude that chicks pay attention to the width of the spectrum of their parental calls (two frequencies at least are necessary), the important part being the lower frequencies. They may use low frequencies because high frequencies cannot be transmitted far in the atmosphere without strong attenuation (Wiley & Richards 1978) and the background noise is so loud that a call cannot be heard more than 16–18 m away (Jouventin 1982; Aubin & Jouventin 1998). Moreover, high frequencies cannot be propagated through penguin bodies (Robisson 1991).

Our results also show that chicks are sensible to the effects of shifting frequency: significant differences were obtained with changes of as little as 25 Hz (for example between +75- and +50-Hz signals and +100- and +75-Hz signals). Nevertheless, signals shifted 100 Hz down or 75 Hz up still elicited a majority of positive responses (ranked 2–4 in intensity).

Our experiments showed that AM alone was not sufficient to elicit recognition, even though such a

signal respects the harmonic structure and the temporal succession of syllables of the parental call. In contrast, a signal in which the parental AM was suppressed was recognized without ambiguity by all the chicks tested. These experiments prove that FM is a key feature for the recognition of the parental call, whereas AM is not used for individual recognition. The information content of the FM is concentrated at the level of the syllable since recognition occurred when only one syllable of the parental call was broadcast (signals Sy1 and Sym), whatever the syllable (the first or a syllable in the middle of the call). In fact, it seems that the first half of the syllable was sufficient for recognition. In contrast, the second part of the syllable was not recognized by the chicks. With regard to the FM structure of a syllable of a parental call, it appears that the basic shape is always the same: an increase followed by a decrease in frequency. For all the parental calls that we have analysed, the inflexion point between the increase and decrease in frequency was always contained in the first half of the syllable. It seems that this inflexion point is necessary to elicit recognition. When the inflexion point was lacking, as with the first quarter or the second half of the syllable (signals Q1Sy1 and H2Sy1), the signal was not recognized. The shape of the increasing and then decreasing frequency of the first half of the syllable should correspond to the vocal signature of the call. These results with chicks parallel previous findings with adult king penguin calls. Derenne et al. (1979) and Robisson (1992) performed field playback experiments in which they tested the ability of adults to recognize their mates. They played back reversed calls or signals whose pitch and duration of syllables had been more or less modified and in all cases individual recognition failed. In these experiments, the FM signature of the syllable was modified. As for recognition between mates, the recognition of the parent by the chick seems to be linked to the FM shape of the syllable, which is repeated as a vocal signature on the different syllables of the call.

Adaptation to the Noisy Environment of the Colony

Problems of animal communication in noise can be analysed in engineering terms (Okanoya & Dooling 1991). Two methods used in communication engineering are used to study sensory filtering in animals from the receiver's point of view: the frequency-based filter model and the matched filter model (Hopkins 1983). In a frequency-based filter the output signal corresponds to the correlation between the spectrum of the input signal and the gain of the filter. Such examples of correlations between the acoustic signal and behavioural and auditory thresholds are numerous in birds (Konishi 1970; Dooling et al. 1971; Dooling & Saunders 1975; Okanoya & Dooling 1988). In the matched filter model, the output of the filter corresponds to the cross-correlation between the received and expected signals (an internal template). The existence of this model is suggested by some studies (for example Gaioni & Evans's 1986 study of the distress call of mallard ducklings, *Anas platyrhynchos*). It is likely that king penguin chicks use matched filtering to detect the

parental call embedded in the masking noise of the colony. Effectively, signals with reversed syllables or without FM or without the inflexion point (in the FM structure) did not elicit recognition. On the other hand, signals strongly shifted up or down in frequency did elicit positive responses, and this fails to support the notion that chicks were using frequency-based filters. Cross-correlation detection by matching filtering is known to be the most sensitive method for detecting a signal in noise (Lee 1960). The use of this method of detection should explain why chicks are able to extract the parental call even when call intensity is well below that of the noise of simultaneous calls produced by other adults in the colony (Aubin & Jouventin 1998). In humans, this process of acoustic recognition against a background noise has been called the cocktail-party effect (Cherry 1966) and several authors have suggested its occurrence in animals (Busnel 1977; Wiley & Richards 1982).

Another important point concerns the redundancy of the information. The parental call corresponds to a succession of syllables with a broad frequency band. Our experiments showed that the receiver needs only a small part of the information to recognize the call: chicks identified the parental call with only the first two harmonics, with one syllable and even with the first half of a syllable, a time period less than 6% of the total signal duration (230 ms for a signal of 4–5 s mean duration). Thus the king penguin call is highly redundant in time and frequency. Why such a high redundancy? The background noise of the colony is almost continuous and windows of silence are scarce and unpredictable, for example during a 4-min recording made in a feeding area (unpublished data), only 15% of the time corresponded to relatively quiet periods and the mean duration of these periods of silence was 0.6 s. The adult cannot predict when and for how long it can be heard without jamming. To enhance the chance of feeding its chick, the adult repeats the same information many times and, therefore, has the opportunity to find a window of silence. In terms of harmonic structure, some parts of the spectrum are more or less modfied, depending on the conditions of propagation of the signal, for example, distance, the screening effect of penguin bodies. In this case, if important parameters, such as the frequency modulation, are distributed over many harmonics, these redundant elements of information are more likely to be transmitted without destruction. According to the theory of information (Schannon & Weaver 1949), such high redundancy improves the probability of receiving a message in a noisy channel.

Lastly, the parental call of the king penguin comprises three to seven syllables (Jouventin 1982), each syllable being separated by deep declines in amplitude which appear as silences. These sharp amplitude variations, corresponding to a succession of syllables, are easily distinguished from continuous noises such as wind or sea waves. They also have the advantage of increased locatability (Wiley & Richards 1982) which in turn helps the receiver to detect the signal in the background noise. This is important for king penguins, which do not have a nest site. All the chicks responded with a score of 4 to the

natural parental call and with a score of 2–4 for modified signals such as low pass, without AM or one-syllable signals. These results do not necessarily imply that these modified signals are recognized less; instead they could be more difficult to locate (class 4 response corresponding to an approach oriented towards the loudspeaker).

With an FM signature highly redundant in time and frequency, the code of the king penguin call can thus be regarded as a functional code increasing the possibility of individual recognition in an acoustically constraining environment.

Biological Significance of the Code

Parent–offspring recognition by acoustic signals has been amply documented for birds, and particularly for birds with nests (Falls 1982; Beecher 1989). Often, discussions have emphasized the parents' need to recognize offspring but have neglected pressures for young to recognize parents (Beecher et al. 1985), especially in species without a nest site, such as king penguins. Derenne et al. (1979) showed that parents were able to recognize the call of their young and we have now shown that chicks also recognize the FM signature of the parental call. This recognition process supposes that three conditions are fulfilled.

(1) The chick must learn the parental call. As a result, the call of the parent forms a template (Slater 1989) that, according to the matched filter model described above, the chick correlates (compares) with each received call. In numerous birds, parent–young recognition is effective when young become mobile (Falls 1982; Williams 1982; Böhner 1990), for example the Adelie penguin, *Pygoscelis adeliae* (Jouventin & Roux 1979). The young king penguin has the opportunity to memorize the call of its parent during its first 5 weeks when it remains on the parents' feet, and maybe before, during hatching. Each time a parent returns from foraging to meet its mate, it gives a call for mutual identification, and this call, heard by the chick, is identical to the one the chick later uses to identify its parent (Jouventin 1982).

(2) The FM signature must offer a sufficient number of variations to ensure recognition of each individual and avoid confusion with others. Beecher (1982, 1989) developed a quantitative method for measuring the information capacity needed in a signature system to identify each member of a population with a small probability of confusion. In our case, it was difficult to calculate the theoretical number of possible features of FM signatures. Effectively, an FM signature allows an almost infinite number of combinations between temporal and frequency parameters, far more than that necessary under natural conditions to ensure individual recognition in the colony. In addition, there could be fewer FM signatures than adults in the colony since chicks meet their parents on a rendezvous site, so limiting the probability of confusion.

(3) The FM signature of the parents must be sufficiently stable during the year. The chick must learn at least one FM signature contained in the call of each parent and must be able to distinguish these parental signatures from others. This is a complex learning process. A parental signature system that continually changed would be very confusing for the chick. Previous findings indicate that king penguins do not change their calls: the temporal and frequency features of the calls remain remarkably constant during the year (Jouventin 1982) and even from year to year (unpublished data). Nevertheless, in some species of seabirds, the calls vary continuously. Learning of parental calls by chicks appears to be a countinuing process in the laughing gull, *Larus atricilla* (Beer 1979), for example; this species has nest sites, however, so landmarks limit the possibility of confusion and facilitate individual recognition.

The evolution of coding and decoding sounds may be determined by phylogeny or ecology. The penguin family uses the largest range of breeding sites known for colonial breeding species: (1) burrows as in the little penguin, *Eudyptula minor*; (2) nests made with stones, grasses or branches as in the majority of penguins (and birds); (3) without a nest but on a site during the brooding phase as in the king penguin; and (4) without a nest and without a site such as the emperor penguin, *Aptenodytes forsteri*, moving with its egg on its feet. Since the two non-nesting species need only vocal cues to identify themselves among several hundred breeders (Jouventin 1982), they constitute good models for individual recognition. In future studies, we intend to compare the acoustic mechanisms of identification of the nesting and non-nesting species to determine if coding-decoding processes are related to the breeding constraints of these four groups of birds.

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