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A memory like a female Fur Seal: long-lasting recognition of pup's voice by mothers

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ABSTRACT

In colonial mammals like fur seals, mutual vocal recognition between mothers and their pup is of primary importance for breeding success. Females alternate feeding sea-trips with suckling periods on land, and when coming back from the ocean, they have to vocally find their offspring among numerous similar-looking pups. Young fur seals emit a 'mother-attraction call' that presents individual characteristics. In this paper, we review the perceptual process of pup's call recognition by Subantarctic Fur Seal *Arctocephalus tropicalis* mothers. To identify their progeny, females rely on the frequency modulation pattern and spectral features of this call. As the acoustic characteristics of a pup's call change throughout the lactation period due to the growing process, mothers have thus to refine their memorization of their pup's voice. Field experiments show that female Fur Seals are able to retain all the successive versions of their pup's call.

Key words: acoustic communication, individual recognition, learning process, Fur Seal, mammals.

INTRODUCTION

In numerous birds and mammal species, parents and offspring have to recognize each other to allow the efficiency of the breeding process (Halliday 1983, Charrier et al. 2001a). This mutual recognition is especially important in species which breed in large groups or colonies since there is here a high risk of confusion between individuals (Aubin and Jouventin 2002). An individual recognition process can be potentially supported by any sensory channel: olfactory, visual, acoustic or other. In colonial birds and mammals, acoustic cues are in most of the cases of primary importance. In penguins for instance, vocal recognition between mates and between parents and chicks is the only way to ensure a reliable meeting (Aubin 2004). In mammals, although the olfactory and visual channels are often used for recognition processes at short distances (Stirling 1971), an acoustic signal is also very effective in many cases such as in pinnipeds (Insley 1992, 2000, Charrier et al. 2002a, 2003a).

One problem raised by acoustic individual recognition is the necessary learning process bound to it. Indeed, even if some of the properties of an acoustic signal emitted by a given individual are somewhat predictable in regards to its species, its age and its sex, this signal has to show cues particular to each individual to support individual identification. This is to say that a parent has always to learn to recognize these individual cues in order to reliably identify the voice of its offspring. And, symmetrically, this learning process occurs also for the young which has to accurately identify parental voices. What is the dynamic of this learning process? What is the minimum period of time necessary to both protagonists – parents and offspring – to learn the voice of each

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other? And besides this, what is the duration of this memory? Very few studies have investigated these questions (Addae et al. 2000, Insley 2000, Charrier et al. 2003b).

In the Amsterdam population of the Subantarctic Fur Seal *Arctocephalus tropicalis*, mothers raise their young on the seashore and alternate feeding sea-trips (duration 2-3 weeks) with lactating periods (a few days) until weaning (duration of the breeding period: 10 months). Like most otariids, care is exclusively maternal and females suckle only their own pup (Boness 1990, Georges et al. 1999). When coming back from the ocean, a mother has to find her pup among several other pups in the colony. The success of a meeting is ensured by a reliable mutual vocal recognition of each female-pup pair (Charrier et al. 2001b). If the mother does not come back from sea – and also in the (hypothetical?) case where individual recognition is not effective –, the pup is condemned to death. Given this strong constraint and the long duration of mother's absence, the Amsterdam Fur Seal constitutes a good model to investigate the dynamic of learning and memory of vocal recognition.

Previous experimental studies have shown that mother-pup acoustic identification is mutual in the Amsterdam Fur Seal (Charrier et al. 2002a, 2003a). On one side, a pup needs only 2-5 days to acquire the ability to vocally recognize its mother (Charrier et al. 2001b) and the implied perceptual processes have been experimentally deciphered (Charrier et al. 2003a). It has also been shown that the duration and the strength of the pup's memory is enough to still allow a reliable mother's voice recognition after 2-3 weeks of separation (Charrier et al. 2002b), corresponding to the duration of a female's sea feeding trip. On the other side, field observations strongly suggest that the female is able to reliably recognize the voice of her young within a few hours following parturition (Charrier unpubl. data) and maybe sooner. However, females may face a potential problem. Indeed, as the acoustic structure of bird and mammal vocalizations usually change throughout ontogeny due to the growing process, it is likely that the characteristics of the fur seal pups' voice are modified from birth to weaning. Mothers must be able to cope with these changes.

The aim of the present paper is to review this problem by answering the following three questions: How does a fur seal mother recognize the voice of her pup? How does a pup's voice change during the suckling period? And how does a fur seal mother deal with these modifications?

DISCUSSION

1) How Does a Fur Seal Mother Recognize Her Pup's Voice?

This question was investigated by playback experiments in the field (Amsterdam Island, Indian Ocean, 37°55'S, 77°30'E) using modified pup calls (Charrier et al. 2002a).

The 'female attraction call' emitted by the pup is a complex sound, with a fundamental frequency (mean 607.6 Hz, n=12) and a harmonic series (4-10 harmonics) (Fig. 1). By comparing the inter-individual and intra-individual variations of a number of call parameters, it appears that several cues may support individual identity. On one hand, some frequency parameters like the fundamental frequency and the frequency with the highest energy have a good potential for individual coding. On the other hand, temporal parameters related to frequency modulation are also good individual markers. However, although the analysis stage allows one to isolate the acoustic cues most likely to encode individuality, it is necessary to confirm, by playback experiments with modified signals, that a parameter found to be individually unique by the analysis is actually used for recognition.

Using natural calls of pups, we made experimental signals by modifying frequency and temporal parameters. Through playback experiments, we assessed the eventual role of each acoustic parameter in the individual recognition process. To test if the whole frequency spectrum is required for an effective recognition of the pup's voice by the mother, two experimental signals were used: the

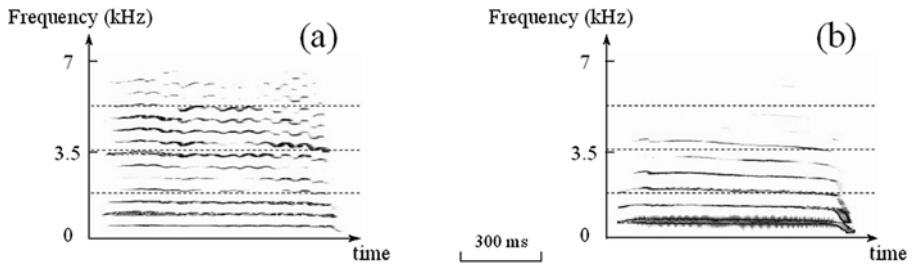

Fig. 1 – Fur Seal pup's 'female attraction call': (a) call of a 1 week-old individual; (b) call of the same individual at the age of 7 months. The acoustic characteristics of the call change throughout the growing period, e.g. only the 1-week call show quavering (see text for details).

first one was high-pass-filtered (all frequencies below 2 kHz were suppressed), the second one was low-pass-filtered (only the frequencies below 2 kHz remained). Results of playback tests using modified signals show that a truncated frequency spectrum still supports individual recognition: mother's recognition ability is unaffected by low-pass filtering of the signals.

Still using playback, we tested how many harmonics are required for the pup's voice recognition by using several experimental signals: one composed of the fundamental frequency and its first two harmonics, one with the fundamental frequency and only the first harmonic, and one consisting of the fundamental frequency alone. It appeared that the fundamental frequency alone is not sufficient to allow reliable recognition; a minimum of two harmonics is necessary. We also investigated the importance of harmonic relationship by testing signals from which every third or every second harmonics had been removed. The results of playback tests show that the distribution of energy within the spectrum is an important feature for individual recognition: when one out of two harmonics is absent, only 60% of mothers still recognize their pup's call.

The frequency and the amplitude modulations of the calls were also studied. Through playback tests, it appears that mothers rely on the frequency modulation pattern to recognize their pup (all females failed to identify their pup's call if it had been experimentally time reversed), and conversely do not pay attention to the amplitude modulation.

To sum up, the recognition of pup calls by fur seal females relies on a multi-parametric analysis of the individual vocal signature of each pup's calls. Two main acoustic features of the call are used. The key one is the temporal frequency pattern since, when this parameter is modified, the recognition process fails. A second one is the distribution of energy among harmonics: the disruption of this parameter also impairs recognition.

2) How Does a Pup's Voice Change During the Suckling Period?

Both call parameters – the frequency modulation pattern and the distribution of energy among harmonics – used in the recognition process are susceptible to change as the pup grows. Indeed, growth-induced modifications in the vocal tract and brain maturation can have consequences for the acoustic structure of the emitted signals (Beecher et al. 1981). We have studied the ontogeny of fur seal pup's vocalizations to detect changes of vocal characteristics, especially those related to frequency modulation and distribution of energy among the frequency spectrum. To do this, several pups were followed and their voice regularly recorded throughout the lactation period, from birth to weaning (Charrier et al. 2003b). Different ages were chosen: less than 1 week old, 1-2 weeks old, 1-3 months old and 5-7 months old. A set of parameters were analyzed

including the value of the fundamental frequency, the values of harmonics corresponding to the first, second and third peak of amplitude and the range of the frequency modulation, We also measured the duration of the quavering part of the call (see figure 1) to fully describe the frequency modulation pattern.

The results first show that, even if the female attraction call emitted by the pup remained a tonal sound composed of a modulated fundamental frequency and its harmonic series, its fine characteristics varied considerably from throughout the growing period. First, the value of the fundamental and the duration of quavering changed with pup's age. For instance, quavering was no longer present after the first two weeks of life. Second, the energy distribution among the frequency spectrum varied according the age. For instance, young pups tended to emit calls with reinforced high-pitched harmonics whereas in older pups the energy of the call was concentrated over the first harmonics.

To sum up, both parameters which have been shown to encode individual identity, i.e. frequency modulation and distribution of energy among harmonics, change from birth to weaning. Since the call characteristics change with the growing process, it is reasonable to assume that the individual signature encoded in it changes also.

3) How Does a Fur Seal Mother Deal With These Modifications?

The modifications of the pup call structure during the growing process are likely to represent a problem for individual voice identification by fur seal mothers. Indeed, just after birth, the female has to learn to recognize the call of her pup. She thus memorizes the acoustic characteristics of the newborn pup's call and relies on these to identify its individual voice. The problem is that these acoustic features will change throughout the growing period and thus the female will have to periodically update the ''recorded'' cues she uses.

By field investigations, we have tested the ability of the female to retain all the successive versions of her pup's call (Charrier et al. 2003b). To do this, we have performed playback experiments just before weaning, asking females if they still recognize the calls which were emitted by their pup at a younger age. The results are unequivocal: females keep the ability to identify their pup's voice whatever its age version. For instance, at the end of the weaning period, i.e. 8-10 months after birth, fur seal females still respond to calls their pups made when they were newborn (less than 1 week old) and ignore any call coming from other pups (Charrier et al. 2003b). Females must thus retain memories of all the successive versions of their pup's voice.

CONCLUSION

The memorization of her pup's voice by the mother fur seal during the breeding period is of outstanding importance since it is a "sine qua non" condition for the female's breeding success. The reliability of this process is an adaptation to the strong ecological constraints imposed on this species. Since the breeding shores are far from oceanic foraging areas, females have to make very long feeding sea-trip during which mother-pup pairs are regularly separated for several weeks. Thus, mothers have to remember the vocal characteristics of their pup's voice for long periods (and the opposite is also true: pups have to remember their mother's voice, the recognition process being mutual).

This ability for long-term memory has also been found in another fur seal species, the Northern Fur Seal *Callorhinus ursinus* (Insley 2000). It has been shown that females are able to identify their pup even some years after weaning. In that case, one can suppose that the pup's voice does not change much during this period. In any case, this ability by another species suggests that the mother's long-term memory of her pup's voice is a widespread characteristic among fur seals.

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RESUMO

Em mamíferos coloniais como as focas, o reconhecimento vocal mútuo entre as mães e seu filhote é de importância primordial para o sucesso reprodutivo. As fêmeas alternam viagens de alimentação no mar com períodos de amamentação em terra e, quando voltam à colônia, elas devem achar vocalmente seu filhote no meio de muitos outros visualmente semelhantes. As jovens focas emitem um ''grito de atração da mãe'' que apresenta características individuais. Examinamos aqui o processo perceptual do reconhecimento do grito do filhote pela mãe numa população sub-antártica da foca *Arctocephalus tropicalis*. Para identificar seu filhote as fêmeas se baseiam no padrão da freqüência de modulação e outras características espectrais deste grito. Como os parâmetros acústicos do grito de um filhote mudam ao longo do período de amamentação por causa do seu crescimento, as mães precisam de uma memorização refinada da voz de seu filhote. Experiências de campo mostram que as fêmeas desta espécie são capazes de se lembrar de todas as versões sucessivas do grito de seu filhote.

Palavras-chave: comunicação acústica, reconhecimento individual, processo de aprendizagem, foca, mamíferos.

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