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Acoustic communication in noise: regulation of call characteristics in a New World monkey

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Summary

This study on common marmosets *Callithrix jacchus* is the first to examine noise-dependent mechanisms of vocal plasticity in a New World monkey. Since acoustic communication can be considerably impaired by environmental noise, some animals have evolved adaptations to counteract its masking effects. The studied marmosets increased the sound level of their spontaneous calls in response to increased levels of white noise broadcast to them. Possibly, such noise-dependent adjustment of vocal amplitude serves to maintain a specific signal-to-noise ratio that is favourable for signal production. Concurrently, the adjustment of vocal amplitude can maintain a given active space for communication. In contrast to some bird species, no noise-induced increase in the number of syllables per call series could be found, showing that an increased serial redundancy of vocal signals was not used to communicate under noisy conditions. Finally, we examined a possible noise-dependent prolongation of vocal signals. This approach was guided by the findings of perceptional studies, which suggest an increased detection probability of prolonged signals in noise by temporal summation. Marmosets indeed increased the duration of their call syllables along with increasing background noise levels. This is the first evidence of such mechanism of vocal plasticity in an animal communication system.

Key words: acoustic communication, environmental noise, signal masking, vocal plasticity, Lombard effect, common marmoset, *Callithrix jacchus.*

Introduction

The exchange of information between individuals by acoustic signals is considerably constrained by environmental factors. In their comprehensive review, Wiley and Richards (1982) summarized the properties of the habitat that limit signal transmission and showed that signals are subject to temporal and spectral degradation as well as frequency-dependent attenuation while travelling through the environment. In turn, the attenuation affects the signal propagation, and the signal intensity decreases with increasing distance from the emitter. When the signal amplitude is reduced to the level of the sensory threshold of the receiver, the maximum transmission distance is reached, which determines the broadcast area, or active space, of the signal. The issue of active space has received much attention in research on acoustic communication, and studies estimating the communication range have been conducted in birds and mammals (e.g. Brenowitz, 1982; Brown, 1989a; Janik, 2000). However, it is important to be clear that the communication range is not only determined by the absolute signal amplitude. The level and spectral characteristics of background noise also play important roles, because detection and recognition of signals substantially depend on the signal-to-noise-ratio (Klump, 1996). In the natural environment most vocalizing animals have to face the masking effects of abiotic noise (caused, for example, by wind, rain, flowing water or surf), as well as biotic noise, i.e. interfering sounds produced by other animals. Biotic noise may be the acoustic signals of other species, or the sounds uttered by conspecifics, as it is the case in colonial birds (e.g. Moseley, 1979; Aubin and Jouventin, 2002) and chorusing insects or anurans (reviewed in Gerhardt and Huber, 2002), where a vocalizing animal has to obtain a hearing before the background of a multitude of vocalizing conspecifics.

In some habitats acoustic communication is severely impaired by the constant masking of high intensity background noise caused e.g. by fast-flowing streams or waterfalls. An evolutionary response of frogs and birds living in such noisy habitats is to evade masking by producing high pitched vocalizations in narrow frequency-bands (Dubois and Martens, 1984). In addition, many animals evolved short-term adaptations to mitigate interference from more temporary background noise. On this short-term level, two different vocal mechanisms of noise-dependent vocal plasticity have been documented to date. Japanese quail *Coturnix coturnix japonica* (Potash, 1972) and king penguins *Aptenodytes patagonicus* (Lengagne et al., 1999) increase the number of syllables per call series with increasing background noise or wind. This relationship is in line with predictions from information theory indicating that the probability of receiving a message in noise can be improved by increasing the redundancy of the signal (Shannon and Weaver, 1949). It is not known, however, whether mammals counteract interference from background noise by increasing the redundancy of their signals.

Secondly, a signaller may increase the amplitude of its vocalizations in response to an increase in the background noise level. This mechanism of amplitude regulation is termed the ‘Lombard effect’ (Lombard, 1911) and has been shown for birds (Potash, 1972; Manabe et al., 1998; Cynx et al., 1998; Brumm and Todt, 2002), macaques (one pig-tailed macaque *Macaca nemestrina* and one long-tailed macaque *Macaca fascicularis*; Sinnott et al., 1975) and humans (reviewed in Lane and Tranel, 1971). It is not clear to date whether the Lombard effect in the studied primate species reflects a special adaptation of Old World monkeys or whether it is a more widespread form of primate vocal plasticity.

In addition to the increase in amplitude and of redundancy, there might be a third vocal mechanism to counteract masking effects of environmental noise. Perceptional studies in a variety of species have shown that the detectability of brief acoustic signals improved considerably with increasing signal duration (e.g. Johnson, 1968; Dooling, 1979; Brown and Maloney, 1986; Klump and Maier, 1990). This phenomenon is based on the temporal summation of signal energy in the peripheral auditory system of receivers and plays an important role, especially in the detection of acoustic signals in noise, such as in the natural environment. Dooling and Searcy (1985) studied the temporal integration of acoustic signals masked by a background of broadband white noise in budgerigars (*Melopsittacus undulatus*). They found a decrease in the birds’ threshold for the detection of brief pure tones (of duration <200 ms) along with increasing signal duration. To date, temporal summation has been used to explain the evolution of signals of duration 200 ms or more in some species (Klump, 1996). In the context of short-term adaptations, however, one might also reasonably assume that the duration of briefer signals may be individually increased to reduce the masking effects of temporally increased environmental noise. To our knowledge, this hypothesis has not yet been tested.

We investigated the three issues outlined above in a small, arboreal New World monkey, the common marmoset *Callithrix jacchus*. This species is a good model to study the mechanisms of vocal plasticity, not only because common marmosets readily vocalize a lot but also because their vocal repertoire has been described (Winter and Rothe, 1979) and we know much about their production and usage of vocalizations (e.g. Epple, 1968; Schrader and Todt, 1993; Geiss and Schrader, 1996; Hook-Costigan and Rogers, 1998; Norcross et al., 1999).

A call type uttered very often by common marmosets is the twitter call (Fig. 1). It may play a role in group cohesion and consists of very brief syllables (<120 ms; A. Sagüi de Tufos-Brancos, personal communication), which are uttered in homotype call series with varying syllable numbers (Winter and Rothe, 1979). Because of these characteristics and the frequent occurrence of twitter calls, this call type should be particular well suited for the investigation of communication in noise. We studied possible noise-induced changes in marmoset twitter calls by experimentally manipulating the background noise and measuring the sound level of vocalizations, the number of syllables per call series, and the duration of syllables.

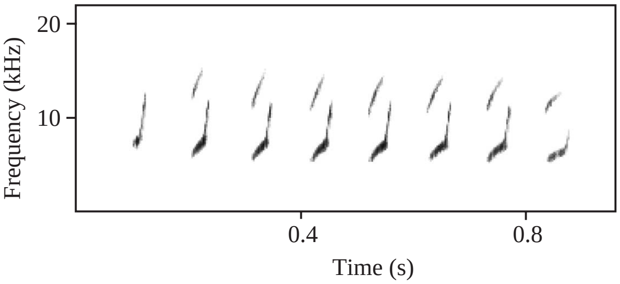

Fig. 1. Spectrogram of a common marmoset twitter call comprising eight syllables.

Materials and methods

Subjects and apparatus

We studied a group of five common marmosets *Callithrix jacchus* L. (4 males and 1 female, aged 9–11 years) housed together in a room (4.7 m × 4.0 m and 2.7 m high) lined with anechoic material. In this room the marmosets were kept in a wire cage (3.3 m × 2.0 m and 2.0 m high, mesh size 2 cm × 2 cm and 1.1 mm wire diameter) enriched with branches and sleeping boxes. This home cage was connected to a test cage (30 cm × 50 cm and 60 cm high) which was constructed with the same mesh wire as the home cage. A small wooden platform (15 cm × 15 cm) allowed one monkey to sit in the test cage. An omnidirectional microphone (Sennheiser ME 62, Wedemark, Germany) connected to a Sony TCD-D3 DAT recorder was placed 55 cm above the platform to record the subjects’ vocalizations. Given the directional sound radiation pattern of most vertebrate vocalizations (e.g. Brown, 1989b; Brumm, 2002), we chose this array to minimize variation in sound level caused by lateral movements of the monkeys’ heads. White (broad-band) noise was generated by a PC with a SB AudioPCI 128 sound card (sampling rate: 48 kHz, accuracy: 16 bit) and recorded on digital tape. The tape was played back with a Sony DTC 670, fed through an amplifier (Technics SU-A600, Osaka, Japan) and then to two loudspeakers with a relatively flat spectrum (Canton PLUS X, Weilrod, Germany; frequency range 45–30 000 Hz). The speakers, mounted on tripods at the height of the platform facing the narrow sides of the test cage, were placed 1 m apart with the platform in the middle between them.

Procedure

At the beginning of each test session a randomly selected level of white noise (40, 50, 60 or 65 dB SPL) or no noise was played back. After 30 min another noise level was randomly chosen. Whenever a marmoset entered the test cage, its identity was recorded as well as its position in the cage when it was vocalizing. This procedure allowed us to analyse only recordings from monkeys sitting on the platform. We conducted one test session on each of three consecutive days. The sound level of the noise playbacks was set according to previous measurements of the playback level done with an EZGA 2 (Rohde & Schwarz, München, Germany) precision sound level meter (using the time constant 'Fast' and a linear frequency weighting, measuring frequency range 10–25 000 Hz) at the position of the platform in the test cage. For these measurements the volume of the amplifier was changed and the given sound level was controlled with the sound level meter at the position normally occupied by the monkey's head. The ambient noise level (when no white noise was broadcast) was ca. 30 dB SPL (measured as described above).

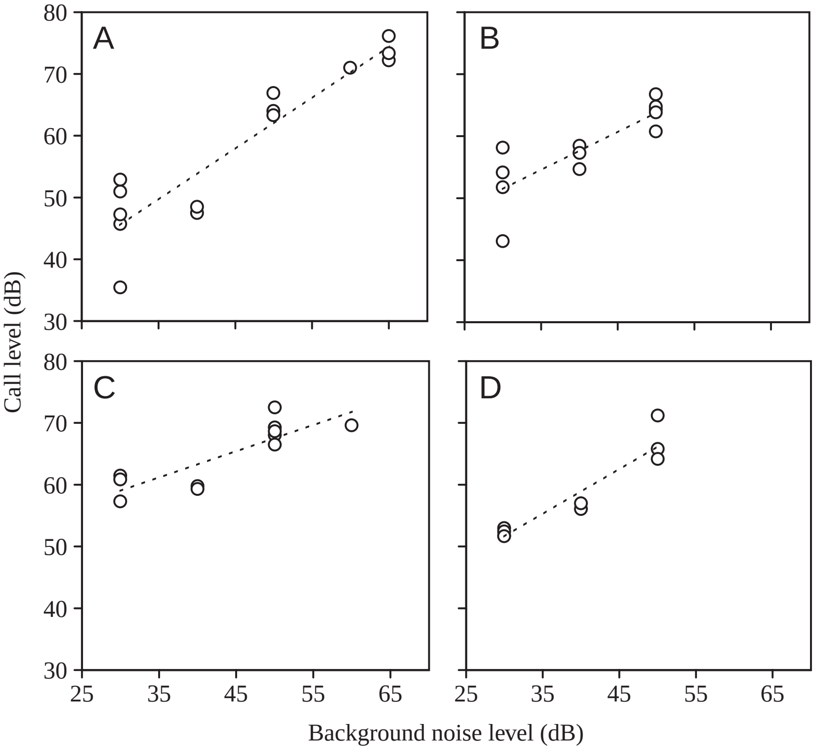

Fig. 2. Regulation of the call level by common marmosets. Each data point represents the median value of one twitter call series (dB re. 20 μPa). (A) Female: r_s=0.904, N=14, P_c<0.001; (B) Male 1: r_s=0.887, N=12, P_c<0.01; (C) Male 2: r_s=0.816, N=11, P_c<0.01; (D) Male 3: r_s=0.935, N=9, P_c<0.01.

Data analysis

We examined the twitter calls of all monkeys that uttered at least one such call series in three different noise conditions. This was the case for three males and the female. The calls of these marmosets were analysed using Avisoft-SASLab Pro software (R. Specht, Berlin, Germany). We digitized the recordings with 16-bit resolution and a sampling rate of 44.1 kHz. For sound level measurements of the recorded calls, Avisoft was calibrated: 2 s of white noise at 65 dB was analysed for each test session and the digitized sound level of the recorded noise was set to the value directly measured with the sound level meter at the position of the microphone. Then the maximum root-mean-squared sound pressure value of each call syllable was measured (with an averaging time of 1 ms). To determine the sound level of each syllable, we finally subtracted the sound level of the added noise (or the ambient noise level when no white noise was added) from the measurements according to the logarithmic computation procedures given in Weißing (1984). The duration of the syllables was measured in sonagrams calculated with a Fast Fourier Transformation-length of 64 points (resulting in a temporal resolution smaller than 2 ms). For the sound level measurements we used only recordings not disturbed by noise produced by the other marmosets, especially their vocalizations. For this reason the sample sizes of the sound level measurements may be smaller than those of the other analyses.

For each individual, we examined the relationship between the measured characteristics of the call series (median sound level, median duration of syllables, and the number of syllables per series) and the background noise level using two-tailed Spearman rank correlations. We used the Dunn–Šidák method (Sokal and Rohlf, 2001) to calculate a-level-corrected P-values (hereafter P_c).

Results

All marmosets increased the median sound level of their twitter calls in response to an increase in the background noise (Fig. 2). In addition, we revealed a second mechanism of noise-dependent vocal plasticity, i.e. the regulation of signal duration. All subjects showed a positive correlation between the background noise level and their median call syllable duration: when exposed to more intense noise, the monkeys uttered longer call syllables (Fig. 3). During the playback of 65 dB white noise the female's median call syllable duration was 65 ms, which corresponds to a syllable prolongation of almost 30% compared to the 40 dB condition (Fig. 3A). The average slope of the psychometric functions of all subjects was 0.59, which corresponds to an average syllable prolongation of 10 ms in response to increase of 17 dB in the background noise level.

In contrast to these noise-dependent changes in call level and call syllable duration, none of the subjects showed any tendency to increase the number of call syllables in response to increased background noise (Fig. 4).

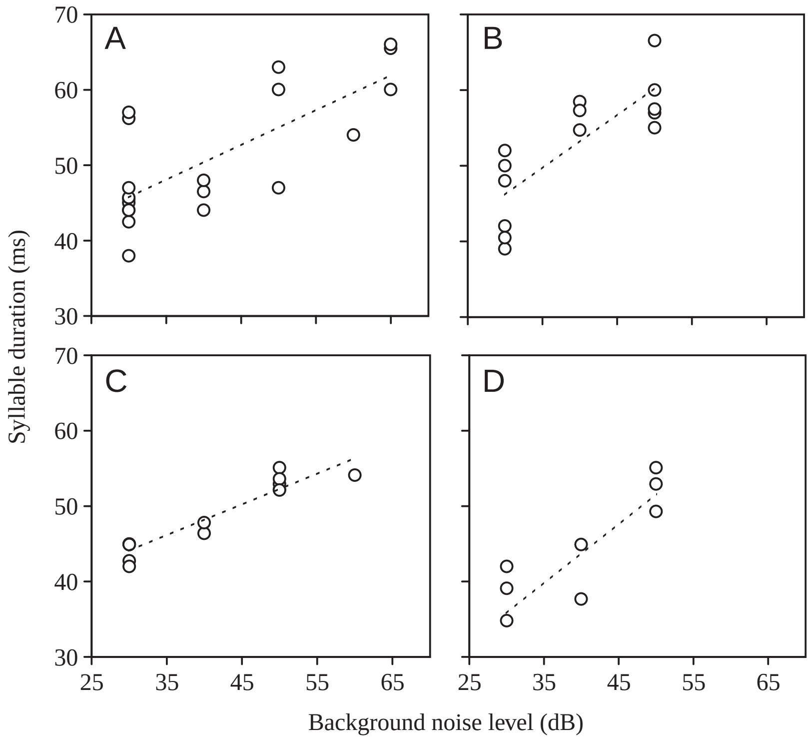

Fig. 3. Regulation of the call syllable duration by common marmosets. Each data point represents the median value of one twitter call series (dB re. 20 µPa). (A) Female: r_s=0.718, N=20, P_c<0.001; (B) Male 1: r_s=0.838, N=14, P_c<0.01; (C) Male 2: r_s=0.924, N=14, P_c<0.0001; (D) Male 3: r_s=0.829, N=9, P_c<0.05.

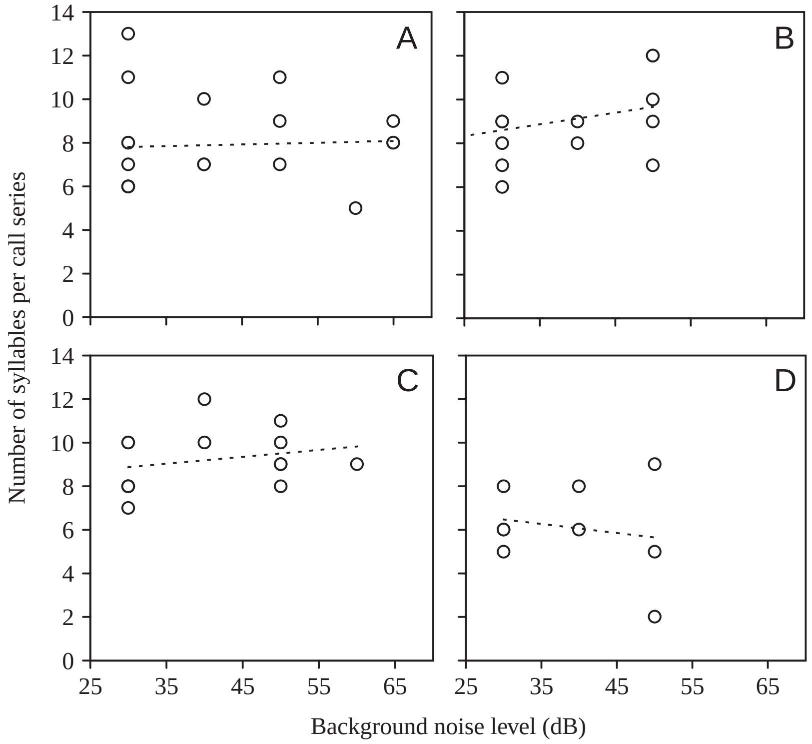

Fig. 4. Number of syllables per call series produced by common marmosets in relation to the background noise level (dB re. 20 µPa). (A) Female: r_s=0.218, N=20, P_c=0.725; (B) Male 1: r_s=0.409, N=14, P_c=0.383; (C) Male 2: r_s=0.285, N=14, P_c=0.689; (D) Male 3: r_s=–0.144, N=9, P_c=0.9919.

Discussion

Our study demonstrates the capacity for multiple vocal adaptations to temporary situations in an animal communication system. Common marmosets increased the amplitude of their twitter calls in response to increased levels of white noise. In addition, we found a prolongation of call syllable duration related to the background noise level. Thus, in this Neotropic primate, vocal amplitude as well as the duration of call syllables are flexible traits, which can be regulated according to ecological demands from signal transmission.

A crucial effect of background sounds on the evolution of frequency traits of animal vocalizations has been suggested for birds and primates (Wiley and Richards, 1982; Ryan and Brenowitz, 1985; Waser and Brown, 1986). Blue monkeys *Cercopithecus mitis* and pygmy marmosets *Cebuella pygmaea* produce calls with dominant frequencies coinciding with typical low-amplitude regions in the environmental noise spectra of their habitats, which may be the result of an evolutionary shaping of call phonetics to minimise masking by background noise (Brown and Waser, 1984; de la Torre and Snowdon, 2002). Furthermore, de la Torre and Snowdon (2002) could show that with varying communication distance, pygmy marmosets use two different call types that transmit particularly well over the respective distance. In addition to this context-specific use of different call types and the evolutionary shaping of signal structure, however, our results demonstrate a primate's capability for individual regulation of the parameters of a given call to mitigate signal masking from background noise. This finding shows that primates can control the production of their vocalizations (at least with respect to signal duration and amplitude).

However, unlike quails and penguins (Potash, 1972; Lengagne et al., 1999), the examined marmosets did not vary the number of syllables per call series in relation to the background noise level. Although there was some variability in the number of syllables, the monkeys did not use an increased serial redundancy of the vocal signals to counteract the communicative constraints of environmental noise.

Our study is the first to report a noise-dependent prolongation of acoustic signals in an animal communication system. This regulation of signal duration is possibly adapted to the perception mechanisms of the addressees, for the detectability of brief acoustic signals increases with signal prolongation, based on temporal summation of signal energy (Watson and Gengel, 1969). Closely related to the perceptional accomplishment of signal detection is the localization of stimuli. Similar to the improved detection in noise, a prolongation of brief sounds can considerably improve their localization (Hofman and van Opstal, 1998; Macpherson and Middlebrooks, 2000). Since marmosets live in forests where visibility is limited, maintaining a sufficient locatability of calls may be crucial for the animals when signalling their position to group mates.

In addition to the noise-dependent prolongation of syllables, the examined marmosets also exhibited the Lombard effect. All monkeys increased the amplitude of their twitter calls in response to increased levels of white noise. Like the prolongation of syllables, this response to background noise helps to counteract the environmental constraints on the communication channel. Hence, our findings show that a New World monkey is able to actively maintain the distance in which another conspecific can perceive its calls. Thus the active space seems to be a dynamic feature rather than a rigid property of a given signal system. As environmental conditions may quickly change, some animals regulate the characteristics of their vocal signals accordingly.

Alternatively, animals could always produce their vocalizations with high amplitudes and durations irrespective of the background noise level. But obviously there is a trade-off between maximising signal transmission and factors that favour inconspicuous vocalizations. Keeping signal amplitude and duration at a low level may reduce the probability of signal detection and localization by unwanted receivers, e.g. predators. Corroborative evidence to support this comes from studies on vocal amplitude in songbirds (Dabelsteen et al., 1998; Brumm and Todt, 2002; Brumm, in press). Finally the reported short-term adaptations in signal production may reflect ways of limiting the energetic costs of vocalizing.

Studies on the Lombard effect are not only of interest for elucidating communication in noise but also for investigating the relationship between hearing and vocal production. In this context, our results provide evidence for a neuronal feedback loop between auditory perception and vocal production in common marmosets. Obviously, monkeys monitor their own vocalizations and assess the intensity of background noise. Thus the adjustment of vocal amplitude may serve to maintain a specific signal-to-noise ratio that is favourable for signal production.

In conclusion, the overall picture shows that the common problem of communication in noise has shaped the common solution of amplitude regulation in all vertebrate taxa tested so far. In addition, some bird species also adjust the redundancy of their signals to mitigate interference from environmental noise. Further studies in different species will show whether the revealed regulation of brief signal durations in common marmosets represents a general mechanism of vocal production in animal communication systems or whether it is a special adaptation of only few taxa.

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References

Aubin, T. and Jouventin, P. (2002). Localisation of an acoustic signal in a noisy environment: the display call of the king penguin *Aptenodytes patagonicus*. *J. Exp. Biol.* **205**, 3793-3798.

Brenowitz, E. A. (1982). The active space of redwinged blackbird song. *J. Comp. Physiol. A* **147**, 511-522.

Brown, C. H. (1989a). The active space of blue monkey and grey-cheeked mangabey vocalizations. *Anim. Behav.* **37**, 1023-1034.

Brown, C. H. (1989b). The measurement of vocal amplitude and vocal radiation pattern in blue monkeys and grey cheeked mangabeys. *Bioacoustics* **1**, 253-271.

Brown, C. H. and Maloney, C. G. (1986). Temporal integration in two species of Old World monkeys: Blue monkeys (*Cercopithecus mitis*) and grey-cheeked mangabeys (*Cercocebus albigena*). *J. Acoust. Soc. Am.* **79**, 1058-1064.

Brown, C. H. and Waser, P. M. (1984). Hearing and communication in blue monkeys (*Cercopithecus mitis*). *Anim. Behav.* **32**, 66-75.

Brumm, H. (2002). Sound radiation patterns in nightingale songs. *J. Orn.* **143**, 468-471.

Brumm, H. (in press). The impact of environmental noise on song amplitude in a territoral bird. *J. Anim. Ecol.*

Brumm, H. and Todt, D. (2002). Noise-dependent song amplitude regulation in a territorial songbird. *Anim. Behav.* **63**, 891-897.

Cynx, J., Lewis, R., Tavel, B. and Tse, H. (1998). Amplitude regulation of vocalizations in noise by a songbird, *Taeniopygia guttata*. *Anim. Behav.* **56**, 107-113.

Dabelsteen, T., McGregor, P. K., Lampe, H. M., Langmore, N. E. and Holland, J. (1998). Quiet song in song birds: an overlooked phenomenon. *Bioacoustics*, **9**, 89-105.

de la Torre, S. and Snowdon, C. T. (2002). Environmental correlates of vocal communication of wild pygmy marmosets, *Cebuella pygmaea*. *Anim. Behav.* **63**, 847-856.

Dooling, R. J. (1979). Temporal summation of pure tones in birds. *J. Acoust. Soc. Am.* **65**, 1058-1060.

Dooling, R. J. and Searcy, M. H. (1985). Temporal integration of acoustic signals by the budgerigar (*Melopsittacus undulatus*). *J. Acoust. Soc. Am.* **77**, 1917-1920.

Dubois, A. and Martens, J. (1984). A case of possible vocal convergence between frogs and a bird in Himalayan torrents. *J. Orn.* **125**, 455-463.

Epple, G. (1968). Comparative studies on vocalization in marmoset monkeys (Hapalidae). *Folia Primatologica* **8**, 1-40.

Geiss, S. and Schrader, L. (1996). Temporal and structural features of infant calls in relation to caregiving behaviour in common marmosets, *Callthrix j. jacchus*. *Behav. Process.* **38**, 183-191.

Gerhardt, H. C. and Huber, F. (2002). *Acoustic Communication in Insects and Anurans*. Chicago, London: University of Chicago Press.

Hofman, P. M. and van Opstal, A. J. (1998). Spectro-temporal factors in two-dimensional human sound localization. *J. Acoust. Soc. Am.* **103**, 2634-2648.

Hook-Costigan, M. A. and Rogers, L. J. (1998). Lateralized use of the mouth in production of vocalizations by marmosets. *Neuropsychologia* **36**, 1265-1273.

Janik, V. M. (2000). Source levels and the estimated active space of bottlenose dolphin (*Tursiops truncatus*) whistles in the Moray Firth, Scotland. *J. Comp. Physiol. A* **186**, 673-680.

Johnson, C. S. (1968). Relation between absolute thresholds and duration-of-tone in the bottlenosed porpoise. *J. Acoust. Soc. Am.* **43**, 757-763.

Klump, G. M. (1996). Bird communication in the noisy world. In *Ecology and Evolution of Acoustic Communication in Birds* (ed. D. E. Kroodsma and E. H. Miller), pp. 321-338. Ithaca: Cornell University Press.

Klump, G. M. and Maier, E. H. (1990). Temporal summation in the European starling (*Sturnus vulgaris*). *J. Comp. Psychol.* **104**, 94-100.

Lane, H. and Tranel, B. (1971). The Lombard sign and the role of hearing in speech. *J. Speech Hearing Res.* **14**, 677-709.

Lengagne, T., Aubin, T., Lauga, J. and Jouventin, P. (1999). How do king penguins (*Aptenodytes patagonicus*) apply the mathematical theory of information to communicate in windy conditions? *Proc. R. Soc. Lond. B* **266**, 1623-1628.

Lombard, E. (1911). Le signe de l'élévation de la voix. *Ann. Mal.Oreil. Larynx* **37**, 101-119.

Macpherson, E. A. and Middlebrooks, J. C. (2000). Localization of brief sounds: Effects of level and background noise. *J. Acoust. Soc. Am.* **108**, 1834-1849.

Manabe, K., Sadr, E. I. and Dooling, R. J. (1998). Control of vocal intensity in budgerigars (*Melopsittacus undulatus*): differential reinforcement of vocal intensity and the Lombard effect. *J. Acoust. Soc. Am.* **103**, 1190-1198.

Moseley, L. J. (1979). Individual recognition in the least tern (*Sterna albifrons*). *Auk* **96**, 31-39.

Norcross, J. L., Newman, J. D. and Cofrancesco, L. M. (1999). Context and sex differences exist in the acoustic structure of phee calls by newly-paired common marmosets (*Callithrix jacchus*). *Am. J. Primatol.* **49**, 165-181.

Potash, L. M. (1972). Noice-induced changes in calls of the Japanese quail. *Psychonom. Sci.* **26**, 252-254.

Ryan, M. J. and Brenowitz, E. A. (1985). The role of body size, phylogeny, and ambient noise in the evolution of bird song. *Am. Nat.* **126**, 87-100.

Schrader, L. and Todt, D. (1993). Contact call parameters covary with social context in common marmosets, *Callthrix j. jacchus*. *Anim. Behav.* **46**, 1026-1028.

Shannon, C. E. and Weaver, W. (1949). *The Mathematical Theory of Communication*. Urbana: Illinois University Press.

Sinnott, J. M., Stebbins, W. C. and Moody, D. B. (1975). Regulation of voice amplitude by the monkey. *J. Acoust. Soc. Am.* **58**, 412-414.

Sokal, R. R. and Rohlf, F. J. (2001). *Biometry: The Principles and Practice of Statistics in Biological Research*. New York: W. H. Freeman and Company.

Waser, P. M. and Brown, C. H. (1986). Habitat acoustics and primate communication. *Am. J. Primatol.* **10**, 135-154.

Watson, C. S. and Gengel, R. W. (1969). Signal duration and signal frequency in relation to auditory sensitivity. *J. Acoust. Soc. Am.* **46**, 989-997.

Weißing, H. (1984). Pegelgrößen. In *Taschenbuch Akustik* (ed. W. Fasold, W. Kraak and W. Schirmer), pp. 380-387. Berlin: VEB Verlag Technik.

Wiley, R. H. and Richards, D. G. (1982). Adaptations for acoustic communication in birds: sound transmission and signal detection. In *Acoustic Communication in Birds*, vol. 1 (ed. by D. E. Kroodsma and E. H. Miller), pp. 131-181. New York: Academic Press.

Winter, M. and Rothe H. (1979). Darstellung des Lautrepertoires handaufgezogener Weißbüscheläffchen (*Callithrix j. jacchus*) unter besonderer Berücksichtigung der fließenden Übergänge zwischen den einzelnen Lautgruppen. *Primates* **20**, 259-276.