The evolution of the Lombard effect: 100 years of psychoacoustic research

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Summary
On the occasion of the centenary of the discovery of the Lombard effect, we review the literature on noise-dependent regulation of vocal amplitude in humans and other animals. The article addresses the scientific and the biological history of the Lombard effect: first, it sketches the evolution of the study of the Lombard effect, and second it reflects on the biological evolution of the effect itself. By comparing the findings from anurans, birds and mammals, we try to trace back the phylogenetic origins of this basic vocal mechanism for acoustic communication in noise. The current evidence suggests two alternative parsimonious hypotheses: either the Lombard effect is the outcome of a convergent evolution in birds and mammals or it may be a synapomorphy of all amniotes. If the latter is true, then the Lombard effect would have evolved to maintain vocal communication in the presence of noise more than 300 million years ago.

Keywords: acoustic communication, auditory feedback, Lombard effect, noise, signal amplitude, vocal plasticity.

“Il est indispensable aussi d’en préciser le sens”
Etienne Lombard (1911) Annales des Maladies de l’Oreille et du Larynx 37, page 119

1. A remarkable discovery
One hundred years ago, the French otolaryngologist Etienne Lombard (Figure 1) published an article based on a peculiar observation he had made while

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Etienne Lombard (1869–1920), a French otolaryngologist and surgeon who discovered the noise-dependent regulation of speech amplitude, which has since become known as the Lombard effect. In brief, the Lombard effect is an involuntary vocal response by speakers to the presence of background noise, in which a person’s voice is raised in response to an increase in the noise amplitude. In the century since its discovery, this phenomenon has achieved importance far beyond what Lombard could have ever imagined. Today, the Lombard effect has been shown in many birds and mammals and it has proven important for the study of acoustic communication in noise in these taxa. Photo by Paul Berger, reprinted from Lermoyez (1920).

Lombard’s discovery was made possible by a device the Austrian physician Robert Bárány had invented, which allowed the delivery of an intense noise to one ear, thus permitting the monaural examination of the other ear (Bárány, 1908). Using this and similar devices, Lombard presented noise to a patient who was engaged in conversation. He found that the person increased his vocal level whenever he was exposed to the noise, and when the
noise stopped, he lowered his voice again to its former level. The patient did not seem to be aware of any change in his vocal effort. In a subsequent series of experiments, Lombard expanded the initial discovery, and he reported his findings in a letter to the French Academy of Science in August 1909, and then to the Academy of Medicine in April 1910. The chronology of these events was of particular interest when Lombard found that his discovery was reported in several scientific publications but attributed to Bárány. This led to a dispute in print between the two scientists in the medical journal *Annales de Maladies de l’Oreille et du Larynx* (Bárány, 1910; Lombard, 1910a,b). Eventually the English physician Donald Schearer wrote a letter to the editor of this journal, in which he disclosed that after he had learned about Lombard’s experiment at the Hôpital Lariboisière, he travelled to Vienna in January 1910 where he informed Bárány about the discovery, who was not aware of it at this time (Sebileau, 1911). So, the matter of priority was settled, and the controversy obviously did not do much harm to Bárány’s reputation — in 1914, he received the Nobel Prize in Physiology or Medicine (although not for work on the Lombard effect). Sadly, Lombard himself was much less fortunate: seven years after the publication of his classic paper, his career was abruptly ended by a painful disease from which he would never recover. Two years later he died at the age of 50, many years before the importance of his work was fully recognized. The distinguished otolaryngologist Marcel Lermoyez concluded his obituary on Lombard with the following bitter words: “In vain has he freely sown, in vain has he laboriously cultivated the field of his activity, if he reaps no harvest; for he never tastes the joys of a fruitful autumn nor the rest and calm of the winter which ends a happy life” (Lermoyez, 1921).

Eventually, several decades after Lombard’s death, his work on the effects of noise on speech amplitude proved important for many different scientific disciplines (Zollinger & Brumm, 2011), such as psychology, neurobiology, linguistics, engineering and last, but not least, animal behaviour.

2. From sign to effect: Lombard’s legacy

Lombard himself saw implications of his discovery in two related areas, and elaborated on these in his original 1911 publication and a following paper (Lombard & Baldenweck, 1916). First, the noise-dependent changes in the
human voice provide a means to diagnose a hearing loss and its simulation. Detecting simulated hearing loss is of particular importance for medicolegal cases. Actually, it was this application of the Lombard effect that was the very reason for the dispute about the discovery of the phenomenon between Bárány and Lombard. Second, the Lombard effect identifies a feedback mechanism between vocal production and perception, which serves to correct speech performance. In both fields, the Lombard effect continues to be widely employed (Lane & Tranel, 1971; Brumm & Slabbekoorn, 2005; Garnier et al., 2010).

Initially, the noise-dependent increase of speech amplitude was termed Lombard sign — Lombard’s doctoral student E. Halphen used the term in his work (Halphen, 1910), which was then adopted by others (Lane et al., 1970; Amazi & Garber, 1982; Huber & Chandrasekaran, 2006). Because the adjustment of vocal intensity happens involuntarily, several authors use the term Lombard reflex (e.g., Egan, 1971; Schultzcoulon & Fues, 1975; Lamprecht, 1988; Junqua, 1996; Zhao & Jurafsky, 2009). However, the noise-dependent regulation of speech amplitude is not a true reflex, i.e., it is not solely mediated via a reflex arc, but also affected by higher cortical areas (see below). Hanley & Harvey (1965) were among the first to name the phenomenon the Lombard effect, and this term is now generally accepted (e.g., Brumm et al., 2009; Zwemer et al., 2009; Garnier et al., 2010; Kim et al., 2010; Love & Bee, 2010; Rindel, 2010).

The changes in terminology also reflect the spread of recognition across disciplines. Initially, studies of the Lombard effect were mainly concerned with hearing tests but since the 1970s medical applications have expanded. Now the Lombard effect is also used in the study of speech and voice disorders (Egan, 1975; Hofler, 1984; Howell, 1990; McColl & McCaffrey, 2006) and as a therapeutic tool for alaryngeal speakers, e.g., following a laryngectomy as patients learn to phonate using sources other than the glottis in the larynx (Zeine & Brandt, 1988; McColl, 2006). A noise-induced increase in vocal amplitude is also used as a treatment to improve the low speech intelligibility in patients with Parkinson’s disease (Adams & Lang, 1992; Ho et al., 1999; Adams et al., 2006; Sadagopan & Huber, 2007). Moreover, the Lombard effect is recognized as a means to experimentally increase vocal effort, e.g., in studies on respiratory kinematics (Winkworth & Davis, 1997; Huber, 2007).
Neurobiological research is not only important to reveal the neuronal substrates underlying the Lombard effect but information on the involved structures is also most informative for the reconstruction of its phylogenetic history. Studies on cats (*Felis catus*) and squirrel monkeys (*Saimiri sciureus*) have shown that the essential neuronal circuits for evoking the Lombard effect in mammals are situated in the brainstem (Nonaka et al., 1997; Hage et al., 2006). More specifically, Hage et al. (2006) discovered particular audio-vocal neurons in the ventrolateral pontine brainstem that may mediate the Lombard effect. These neurons are part of an integration system of vocal production and auditory perception, exhibiting a phasic response to external auditory stimuli. However, this does not necessarily mean that the Lombard effect is a simple reflex, because cortical areas that project, directly or indirectly, to the reticular formation may also be involved (Jürgens, 2009). Indeed, the fact that the Lombard effect can be voluntarily controlled in humans (Pick et al., 1989; Winkworth & Davis, 1997) indicates an involvement of the motor cortex. Moreover, both the linguistic content of the speech (Patel & Schell, 2008; Zhao & Jurafsky, 2009) and the context in which it is used (Amazi & Garber, 1982; Lu & Cooke, 2008; Garnier et al., 2010) affect the degree of voice amplification, showing that higher cognitive processes can be involved in the Lombard effect. In birds, the regulation of vocal amplitude is also quite sophisticated and surprisingly similar to what human speakers do; for example, zebra finches adjust the amplitude of their songs in relation to the distance of the targeted receiver (Brumm & Slater, 2006a).

Forty years ago, Lane & Tranel (1971) reviewed the literature on the Lombard effect and found 63 publications discussing the phenomenon, most of them in connection with hearing tests. Since then, the recognition of Lombard’s work has also spread to other research areas than medicine and psychobiology. As already mentioned above, the Lombard effect is relevant to linguistics and phonetics (e.g., Castellanos et al., 1996; Newman, 2003; Ternström et al., 2006; Gosy, 2007; Patel & Schell, 2008; Zhao & Jurafsky, 2009). Furthermore, in architectural acoustics, the Lombard effect is studied to control noise and to increase speech intelligibility within buildings (Hodgson et al., 2007; Nijs et al., 2008; Rindel, 2010). A particularly prolific application of the Lombard effect in engineering has been in studies on automatic speech and speaker recognition (Junqua, 1993; Hansen & Cairns, 1995; Chi & Oh, 1996; Womack & Hansen, 1999; Bou-Ghazale & Hansen,
Between 1979 and 2009, more than 230 publications referring to the Lombard effect have been published, with a still ongoing increase in publication numbers (Figure 2). This trend is partly due to the increasing number of studies on the Lombard effect in non-human animals.

3. Animal behaviour studies: a comparative view

The study of the Lombard effect in other animals than humans began with Lawrence Potash’s classic work on Japanese quail, *Coturnix coturnix japonica* (Potash, 1972a). Male quails produce so-called separation calls when isolated from their female mate. Potash recorded these separation calls of males in an acoustic chamber with normal ambient noise and while playing back noise (between 0.5 and 5 kHz) at 45 and 60 dB(A). Like the human
patient in Lombard’s experiment, the quails raised the intensity of their vocalizations when the background noise level was increased. Moreover, the Lombard effect was also associated with an increase in the call rate due to higher numbers of crows per call bout (Potash, 1972a,b). Since this initial discovery showing that the Lombard effect is not a uniquely human trait, it has been found in 15 more bird and mammal species (Table 1). In the following, we will apply a comparative evaluation of these data to trace back the phylogenetic history of this auditory feedback mechanism for communication in noise.

Most experimental studies that addressed the Lombard effect in mammals have been on primates, reporting the phenomenon in Old World monkeys (Sinnott et al., 1975) and New World monkeys (Brumm et al., 2004; Egnor & Hauser, 2006). Sinnott et al. (1975) showed that the temporal overlap between vocalization and noise is not enough to induce an increase in vocal sound pressure levels in monkeys but that spectral overlap is necessary. In other words, it is noise overlapping the signal spectrum that is crucial for a Lombard response. The same has also been demonstrated for bird vocalizations (Manabe et al., 1998; Brumm & Todt, 2002).

Recently, Parks et al. (2011) reported the first study showing the Lombard effect in individual whales. The researchers recorded the vocalizations of fourteen North Atlantic right whales (Eubalaena glacialis) using archival acoustic recording tags that were attached to the animals. Because the recording tag was fixed on the animal’s body it allowed measuring the sound level of ambient noise at the position of the calling animal as well as the amplitude of the whale’s calls. Parks et al. (2011) found that the sound pressure level of the whale calls correlated positively with the intensity of the environmental noise. North Atlantic right whales are among the most endangered whales in the world, and the impacts of increases in ocean noise levels from human activities are a current area of concern for the conservation of marine mammals (Richardson et al., 1995; Tyack, 2008; Brumm, 2010). Whether the Lombard effect in right whales is sufficient to maintain their communication range in high-noise situations remains to be investigated.

The Lombard effect is not only exhibited in mammalian communication but also in echolocation, as shown by an experimental study on free-tailed bats, Tadarida brasiliensis (Tressler & Smotherman, 2009). When vocalizing in broadband noise, free-tailed bats not only increased their call amplitude but, at the same time, also call duration and bandwidth. Such a coupling of
Table 1. Studies on the Lombard effect in humans and non-human animals.

<table>
<thead>
<tr>
<th>Class</th>
<th>Order</th>
<th>Species</th>
<th>Evidence</th>
<th>Reference</th>
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<td>Primates</td>
<td>Human</td>
<td>Yes</td>
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<td><em>Homo sapiens</em></td>
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<td>Sinnott et al. (1975)</td>
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<td>Common marmoset</td>
<td>Yes</td>
<td>Brumm et al. (2004)</td>
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<td></td>
<td></td>
<td>Cotton-top tamarin</td>
<td>Yes</td>
<td>Egnor &amp; Hauser (2006)</td>
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<td><em>Saguinus oedipus</em></td>
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<tr>
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<td>Domestic cat</td>
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<td>Parks et al. (2011)</td>
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<td>Leonard &amp; Horn (2005)</td>
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<td></td>
<td></td>
<td>Bengalese Finch</td>
<td>Yes</td>
<td>Kobayasi &amp; Okanoya (2003a,b)</td>
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<td>Psittaciformes</td>
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<td>Yes</td>
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<td></td>
<td>Galliformes</td>
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<td>Potash (1972a)</td>
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<td>Yes</td>
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<td>Tinamiformes</td>
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<td>Yes</td>
<td>Schuster, Lesku, Zollinger &amp; Brumm, unpublished data</td>
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<td><em>Eudromia elegans</em></td>
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<td>Amphibia</td>
<td>Anura</td>
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<td>Love &amp; Bee (2010)</td>
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<td></td>
<td></td>
<td><em>Hyla chrysoscelis</em></td>
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call parameters can also be observed in human speech, monkey calls and bird vocalizations (see below).

In contrast to many mammals, birds rely less on olfactory communication and the acoustic channel plays an even more important role. Indeed, many bird species use vocal signals to defend a territory or attract a mate (Catchpole & Slater, 2008), which means that variation in the efficiency of signalling has major fitness consequences (Brumm & Naguib, 2009). Like humans, many songbirds depend on auditory feedback to precisely control their vocalizations (Wooley, 2008) and the Lombard effect in birds has been interpreted as both a feedback mechanism for vocal production and an adaptation to maintain signal transmission (Cynx et al., 1998; Manabe et al., 1998; Brumm & Todt, 2002; Kobayasi & Okanoya, 2003b).

So far, the Lombard effect has been found in all bird species tested, including several songbirds, a hummingbird, a parrot, two galliforms and a tinamou (Table 1). Tinamous belong to the Palaeognathae, the most basal group of the extant birds, which suggests that the Lombard effect may be a synapomorphic trait of all living birds. Given the generic distribution of the Lombard effect in birds, it is not surprising that the effect is independent of the ontogenetic origin of the vocalization, as it occurs in both vocalizations that are acquired by vocal production learning (Cynx et al., 1998; Brumm & Todt, 2002) as well as those that are not (Potash, 1972a; Cynx et al., 1998; Leonard & Horn, 2005; Brumm et al., 2009). A study on Bengalese finches (*Lonchura striata domestica*) suggested that males of this species show the Lombard effect only in undirected (solo) song but not in directed (courtship) song (Kobayasi & Okanoya, 2003a). However, this pattern was not consistent in all six subjects tested in this study. Moreover, two other studies on the closely related zebra finch (*Taeniopygia guttata*) demonstrated a Lombard response also in directed songs (Cynx et al., 1998; Zollinger et al., 2011). In humans, however, it is well-established that the Lombard effect varies with the social context and speaker task (Amazi & Garber, 1982; Lu & Cooke, 2008; Garnier et al., 2010), indicating that regulation of speech amplitude is not just a simple auditory feedback mechanism. It has also been found that men and women may differ in the strength of the Lombard effect, with women increasing their vocal effort more strongly than men (Egan, 1972). Kobayasi & Okanoya (2003b) reported a similar sex difference in the noise-dependent regulation of call amplitude in Bengalese finches, but in this case males showed a stronger Lombard response than females. Both results can
be explained by the fact that women and male finches used considerably lower amplitudes when no noise was present and, thus, had to raise their voices much more to reduce masking when they were exposed to noise in the experiments.

The remarkable diversity of taxa exhibiting the Lombard effect has led to the view that noise-dependent regulation of voice amplitude is a common trait of vertebrates (e.g., Penna & Hamilton-West, 2007; Tressler & Smotherman, 2009). However, a recent study on Cope’s grey treefrogs (*Hyla chrysoscelis*) revealed that this is not the case (Love & Bee, 2010). Frogs show an important precondition for the Lombard effect, i.e., individuals can vary the amplitude of their calls (Lopez et al., 1988; Penna et al., 2005) but Love & Bee (2010) found no evidence that they use this capacity for communication in noise. While experimentally increased noise levels induced predictable changes in Cope’s grey treefrog call duration and rate, males of this species did not regulate call amplitude. The absence of the Lombard effect in anurans has important implications for our understanding of the evolution of this vocal mechanism, and there has been some controversy in the literature recently over whether or not the Lombard effect has been demonstrated in this group. Penna et al. (2005) have run similar experiments in several frog species and found a lack of a Lombard effect. However, the authors re-evaluated their conclusion in a later paper (Penna & Hamilton-West, 2007) but it is questionable whether the data actually allow assuming a Lombard effect in the studied species (see Love & Bee (2010) for a critique).

We are not aware of any study that reports evidence for a Lombard effect in insects but it is likely that a noise-dependent regulation of signal amplitude is also absent in this taxon. Probably, a convergent evolution of a Lombard effect has not occurred in insects because there seems to be very strong selection for increased loudness of acoustic signals in this group (Gerhardt & Huber, 2002). Thus, in contrast to birds and mammals, insects are perhaps often signalling close to the limits of their power capabilities, which would leave only little room for a Lombard effect. Moreover, like many frog species, insects often call in aggregations, in which males mutually mask their signals (Greenfield, 2005), and in such chorusing species a Lombard effect would quickly escalate, driving all males of the aggregation to signal at maximum levels.

Some methodological issues with regard to testing the Lombard effect in animals are discussed in the Appendix.
4. Signal changes associated with the Lombard effect

The current evidence shows that the common problem of communicating in noisy environments has led to the common solution of the Lombard effect in birds and mammals (Zollinger & Brumm, 2011). In human speech, a suite of vocal changes is often associated with the Lombard effect and combined these changes are referred to as ‘Lombard speech’. Lombard speech includes not only an increase in amplitude, but also a rise in pitch and other spectral changes (see below), and a lengthening of word duration. Some of these additional forms of noise-dependent signal changes associated with the Lombard effect have also been found in other taxa. Humans (e.g., Van Summers et al., 1988; Tartter et al., 1993; Castellanos et al., 1996; Newman, 2003) and monkeys (Brumm et al., 2004; Egnor & Hauser, 2006) increase the duration of brief vocalisations of a few hundred milliseconds, which increases detection and recognition of the signals in noise (Brumm & Slabbekoorn, 2005). A similar effect has been demonstrated in budgerigar contact calls (Osman-ski & Dooling, 2009) and begging calls of nestling tree swallows (Leonard & Horn, 2005). No evidence for a noise-dependent change of call duration was found in domestic fowl (Brumm et al., 2009), indicating that this trait is less widely spread than the Lombard effect itself.

Numerous studies have reported in the last several years that birds in noisy cities sing at higher frequencies, arguing that this is an adaptation to reduce masking from low-frequency traffic noise (e.g., Slabbekoorn & Peet, 2003; Fernández-Juricic et al., 2005; Slabbekoorn & den Boer-Visser, 2006; Wood & Yezerinac, 2006; Bermudez-Cuamatzin et al., 2009; Luther & Baptista, 2010; Salaberria & Gil, 2010). Moreover, experimental studies found that singing birds can vary their songs in response to noise playback either by changes in frequency or changes in song type (Halfwerk & Slabbekoorn 2009; Verzijden et al., 2010; Bermúdez-Cuamatzin et al., 2011). However, none of these studies have measured song amplitude and most of them neglect that an increase in pitch, or change in the spectral slope can be a by-product of the Lombard effect, as is the case in human speech. Spectral slope measures the slope of the energy distribution across frequencies within a vocalization. It is a measure of the relative amplitude of various frequency components in a broadband signal, for example a sound in which the sound energy of the fundamental frequency is high, while the first, second and third harmonics have relatively less energy would have a steep or large spectral
In Lombard speech, there is relatively more energy in the higher harmonics than in quiet speech, and so the spectral slope is smaller, resulting in flatter spectra across all frequencies (Cooke & Lu, 2010). When increasing speech amplitude in noise, a speaker often involuntarily raises his or her vocal pitch by flattening the spectral slope (increasing the relative energy of upper harmonics) and by increasing the fundamental frequency itself (Draegert, 1951; Gramming, 1991; Junqua, 1993; Castellanos et al., 1996; Lienard & Di Benedetto, 1999; Jessen et al., 2005; Ternström et al., 2006; Zhao & Jurafsky, 2009). This increase in vocal frequency is a passive response that occurs irrespective of any release from signal masking (Lu & Cooke, 2009). In low-frequency noise the upward frequency shift, thus, creates a fortuitous masking release. The same may be true for the increase of song pitch in urban bird song. Indeed, several studies have found that amplitude and pitch can be coupled in bird vocalizations (Nelson, 2000; Beckers et al., 2003; Goller & Cooper, 2008; Osmanski & Dooling, 2009; Ritschard & Brumm, in press). Hence, when exhibiting the Lombard effect in noisy environments, a bird’s voice may passively raise in pitch (Brumm & Naguib, 2009; Verzijden et al., 2010). In low-frequency noise typical of cities, these higher pitched songs may be partially released from masking, which would indeed make signal transmission more efficient. If the production of high pitched city songs is driven indirectly by selection on song amplitude, the masking release would be a coincidental by-product of higher amplitude. Additional evidence supporting this notion comes from a study that modelled communication ranges of great tit (Parus major) song (Nemeth & Brumm, 2010). Although great tits can detect high-frequency vocalizations more easily in low-frequency noise (Pohl et al., 2009) the actual benefits of high-pitched songs for signal transmission in noise are very small in comparison to an increase in vocal amplitude (Nemeth & Brumm, 2010). Thus, the current evidence suggests that the often-observed increase of song pitch in urban birds could be an epiphenomenon of the generic Lombard effect, which creates a fortuitous masking release in low-frequency noise, rather than the outcome of direct selection on song pitch.

The mathematical theory of communication indicates that in noisy conditions, the amount of information transmitted can be maintained by an increase of signal redundancy (Shannon & Weaver, 1949). Indeed, Japanese quail (Coturnix coturnix japonica), king penguins (Aptenodytes patagonicus) and chaffinches (Fringilla coelebs) produce more redundant signals
The evolution of the Lombard effect

5. Evolution of the Lombard effect

The current evidence shows that the Lombard effect is present in birds and also in mammals (although a publication bias for positive results can, of course, not be ruled out). Within mammals it is documented in Laurasiatheria and Euarchontoglires, suggesting that the common ancestor of the two clades exhibited it as well (Figure 3a). This means that, according to one of the latest phylogenies of mammal evolution (Bininda-Emonds et al., 2007), the Lombard effect in this group evolved more than 100 million years ago. However, the mechanism for a noise-dependent regulation of vocal amplitude may be much older than this. If it is a shared trait of all mammals, then it has evolved at least 166 million years ago. To establish the Lombard effect...
as an apomorphy for all mammals — and not only therians for which it has been reported to date — it would be necessary to demonstrate it in marsupials and montremes (Figure 3a). In birds, the current evidence implies that the Lombard effect is an apomorphy for all living avian taxa, for it is found in all species tested so far, including one of the most basal bird groups (Table 1, Figure 3b).

Presuming the Lombard effect is a shared trait in all mammals and all birds, one can put forward at least two alternative phylogenetic scenarios: the Lombard effect is either an analogous trait that evolved independently in the two clades or it is a synapomorphy of birds and mammals (Figure 4). The fact that the basic neuronal substrate for the Lombard effect in mammals is located in the brainstem (Nonaka et al., 1997; Hage et al., 2006) might hint at the possibility that the Lombard effect is evolutionarily homologous in birds and mammals. The neuronal circuits essential for the Lombard effect are located in the transition between the midbrain and the pons (Hage et al., 2006). These areas are part of the brainstem, one of the phylogenetically oldest parts of the brain that is highly conserved in birds and mammals.

**Figure 3.** The Lombard effect in birds and mammals. (a) Major mammalian lineages (phylogentic tree is based on Bininda-Emonds et al., 2007), (b) major avian lineages (phylogentic tree is based on Sibley & Ahlquist, 1990). Plus (+), Lombard effect present; question mark (?), character state not documented.
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Figure 4. The Lombard effect in tetrapods. Plus (+), Lombard effect present; minus (−), Lombard effect absent; question mark (?), character state not documented. Parsimonious hypothesis would be that the Lombard effect is either a convergent character in birds and mammals that evolved independently in both clades (black circles) or a synapomorphy for amniotes, i.e., it was present in the common ancestor of birds and mammals (grey circle). This amniote stem species might have looked similar to the artistic reconstruction of *Westlothiana lizziae* (drawing by Arthur Weasley) shown below the cladogram. This species is an extinct tetrapod that lived during the early Carboniferous period. Phylogenetic analyses place *Westlothiana* close to the stem of amniotes (Reisz, 1997; van Tuinen & Hadly, 2004). This figure is published in colour in the online edition of this journal, which can be accessed via http://www.brill.nl/beh
If the Lombard effect is indeed a synapomorphy of birds and mammals, then it should be present in all other amniote species that use vocalizations to communicate, i.e., members of the orders Testudines, Squamata and Crocodylia. Lombard experiments with vocally active reptiles, such as crocodiles or geckoes, pose an excellent opportunity to test this phylogenetic hypothesis. The possibility that the Lombard effect is a synapomorphic character of sauropsids and mammals also implies that vocal communication is an ancestral trait of amniotes. This is not impossible, given that many amphibians use mating calls too. So perhaps, some 320 million years ago the first animal raised its voice to overcome the ambient noise in a carboniferous forest.

The study of Love & Bee (2010) suggests a lack of the Lombard effect in amphibians, although more studies on other species are needed to corroborate the absence of a noise-dependent regulation of vocal amplitude in this clade. However, based on the current evidence it seems parsimonious to assume that the Lombard effect has evolved in amniotes. Studies on fish may or may not reveal a convergent phenomenon in some species of this group. Given the growing interest in the effects of noise on fish communication (e.g., Ladich, 2008; Slabbekoorn et al., 2010) the lacking data will hopefully be published in the near future.

6. Conclusions

The Lombard effect is not only a vivid example of the plasticity of animal behaviour in fluctuating environments but also a particularly informative one, demonstrating the flexibility of acoustic communication systems to facilitate the reception of signals under challenging conditions. The current evidence shows that the common problem of communicating in noisy environments has led to the common solution of the Lombard effect in birds and mammals. As such, the Lombard effect is an important mechanism for acoustic communication in noise, and we encourage investigators not to neglect amplitude regulations when studying the effect of noise on vocal signalling in these taxa. In some species, additional changes of signal features are associated with the Lombard effect, which may increase the detectability and recognition of vocalizations in noise. The evidence for a lack of the Lombard effect in anurans suggests that this basic vocal mechanism has probably
evolved in amniotes, either as a synapomorphy of sauropsids and mammals or independently in the two clades. However, the picture is still patchy. To establish the Lombard effect as a derived trait in birds and mammals it would be necessary to investigate a possible noise-dependent vocal feedback mechanism in marsupials and monotremes, as well as testudines, squamates and crocodilians.

Over the last century the study of the Lombard effect has come a long way, from an accidental observation on a patient in an otolaryngologist’s surgery to modern comparative psychoacoustics. Future studies will hopefully shed more light on the evolution of the Lombard effect, and resolve both the phenomenology and the underlying neurobiological control in different animal clades.

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Appendix: methodological issues of Lombard tests with animals

There are two types of investigations of the Lombard effect in nonhuman animals: correlational studies that measure vocal amplitude as a function of ambient noise amplitude (often
made in free-ranging animals in the wild) and experimental studies that manipulate ambient noise levels and measure vocal amplitude (often conducted in acoustic laboratories). Obviously, the latter are superior in terms of inferences about cause-effect relationships between background noise and vocal amplitude, and are, in general, easier to conduct in a way that produces accurate results. However, both approaches are potentially fraught with methodological errors. In the following we will briefly highlight some of the common pitfalls and how researchers can avoid them.

A.1 Calculating the signal amplitude in background noise

To accurately measure the vocal amplitude, or the level of the signal itself it is necessary to subtract the background noise from that of the signal using logarithmic computation rules (Weißing, 1984). In order to do this, two measurements must be made, one of the total sound pressure level ($L_{\text{sig}+\text{noise}}$) and one of the background noise level alone ($L_{\text{noise}}$). The SPL of the signal itself ($L_{\text{sig}}$) can then be calculated using this formula:

$$L_{\text{sig}} = 10 \log_{10} \left( 10^{(L_{\text{sig}+\text{noise}}/10)} - 10^{(L_{\text{noise}}/10)} \right)$$

A.2 Distance from the sound source to the microphone

Sound amplitude diminishes over distance, making it essential to standardize the distance between the sound source and the microphone if one is to compare amplitudes between different recordings. This can be accomplished either by ensuring the microphone is at a fixed distance relative to the sound source, or by carefully measuring the distance between source and microphone for each recording, and then calculating the amplitudes at a normalized distance. For example, the SPL of a signal normalized to a standard distance of 1 m from the source ($L_{1\text{m}}$) can be calculated using the formula:

$$L_{1\text{m}} = 6 \log_2(d) + L_d,$$

where $d$ is the distance in meters between the sound source and the microphone, and $L_d$ is the SPL measured at distance $d$. However, this method is prone to considerable inaccuracy if used over a wide range of distances, or in habitats that absorb and scatter sound energy, such as forests. In addition, air temperature, humidity and wind speed can all affect sound transmission and confound accurate amplitude measurements (Embleton (1996) provides a tutorial on correcting for these environmental factors). Ideally, recordings should be made as close to the vocalizing animal, and with as few obstructions as possible.

A.3 Orientation of the animal, vocal directionality

To further complicate measurements, sound does not radiate in uniformly spherical pattern from a vocalizing animal. Sound radiation patterns vary with variations in head and body position and size, with changes in mouth or beak gape, as well as with fundamental frequency (e.g., Larsen & Dabelsteen, 1990; Nelson et al., 2005; Patricelli et al., 2007). For instance, the head and body of the animal will attenuate much of the sound energy behind the animal in the horizontal plane, as the sound radiates from the mouth. These acoustic ‘shadows’ are particularly pronounced for higher frequency sounds (i.e., at frequencies with wavelengths that are smaller than the diameter of the animal’s head) or when the microphone is below the
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Figure A1. Schematized patterns of sound radiation in a vocalizing bird. Sound radiation varies in its directionality depending on the size and position of the head and body, and the frequency of the emitted sound. (a) Typical sound radiation pattern at high frequencies, and below the head and body. (b) Above the head, and at lower frequencies, the sound radiation pattern is more uniform but still directional.

head of the animal (Figure A1a), while at longer wavelengths and in the area above the head, the radiation patterns are more uniform (Figure A1b). To control for this, it is necessary to either measure sound radiation patterns for the study species first and correct for differences in orientation, or to only record from the same angle in relation to the animal’s longitudinal axis. Since the sound radiates in a nearly uniform sphere above the head of the vocalizing animal, recording with the microphone directly above the animal and facing downwards minimizes variation due to the horizontal orientation of the recorded animal. This method is fairly standard procedure for laboratory studies on vocal amplitude in birds and mammals, but is often trickier to accomplish in field settings.

A.4 Social context can confound the interpretation of vocal changes in noise

While it is likely that song amplitudes will be lower in laboratory birds, the social and behavioural conditions can nonetheless be fairly well standardized. However, in field studies the researcher must be careful to assess social variables — such as the number and distance of conspecifics and their behaviour — when making comparisons of song amplitude within and between individuals (Ritschard & Brumm, 2011). Therefore, it is important to consider that observed differences in vocal amplitude may be causally related to differences in the social context rather than the result of a Lombard effect.

A.5 Estimating ‘loudness’ and related problems of terminology or methodology

While our hope in writing this review is that behavioural biologists across disciplines and studying diverse taxa will begin to consider the Lombard effect, and sound amplitude in their research, we feel it important to stress rigor in bioacoustical methodology and terminology. Acoustics, like other branches of physics, is governed by a fixed set of laws and principles, and we do a disservice to ourselves by poor field or laboratory practice, or by confusing terminology. As an example, some studies have used human observers to estimate and rank the relative ‘loudness’ of animal vocalizations. While in colloquial speech ‘loudness’ is often
used interchangeably with ‘intensity’ or ‘amplitude’, they are not equivalent. Loudness is a psychophysical rather than a physical measure of sound, i.e., a psychological correlate of human sound perception (Titze, 1996). Therefore, loudness is a subjective measure that varies between individuals (and between taxa, although as a psychological concept it is obviously difficult to measure how non-humans perceive ‘loudness’). Thus, two sounds of equal intensity may not have equal loudness (Moore, 2003). As such, loudness should never be used as a replacement for objective measurements of sound intensity or amplitude.