

## Review

## The Lombard Effect: From Acoustics to Neural Mechanisms

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Understanding the neural underpinnings of vocal–motor control in humans and other animals remains a major challenge in neurobiology. The Lombard effect – a rise in call amplitude in response to background noise – has been demonstrated in a wide range of vertebrates. Here, we review both behavioral and neurophysiological data and propose that the Lombard effect is driven by a subcortical neural network, which can be modulated by cortical processes. The proposed framework offers mechanistic explanations for two fundamental features of the Lombard effect: its widespread taxonomic distribution across the vertebrate phylogenetic tree and the widely observed variations in compensation magnitude. We highlight the Lombard effect as a model behavioral paradigm for unraveling some of the neural underpinnings of audiovocal integration.

**Vocal–Motor Control and the Lombard Effect**

Understanding the neural underpinnings of vocal–motor control remains a major challenge in neurobiology. A key motivation for clarifying the basic principles of vocal–motor control lies in its relevance to human speech production. One crucial aspect of speech production is the ability to exert real-time control over the acoustic features of vocalizations in response to **auditory feedback** (see [Glossary](#)). Vocal–motor adjustment to auditory feedback, however, is not limited to humans. It operates, in fact, in a wide range of animals. Specifically, several groups of animals, including birds [1,2], bats [3–7], and cetaceans [8], are capable of adjusting the fine spectro-temporal structure of vocalizations. Moreover, growing evidence shows that the vocalizations of primates are not as immutable as has been generally believed [9–15]. A comparative analysis of audiovocal control across model organisms can serve to shed light on the underlying neural mechanisms and bring into focus important questions for future research (see Outstanding Questions). Despite progress on many aspects of auditory and vocal production processes, a clear picture of audiovocal feedback control is lacking, even in the case of one of its most widely studied forms: the **Lombard effect**.

The Lombard effect, by strict definition, refers to a rise in call amplitude in response to increasing ambient noise level [16–18]. It is named after Étienne Lombard, who first described adjustments in vocal amplitude in response to ambient noise over a century ago [19]. Research on the Lombard effect began with an exclusive focus on humans, and these early results were reviewed by Lane and Tranel in 1971 [20]. In the decades since then, research on the Lombard effect has expanded, spanning human and animal studies [21]. In addition to addressing the classic questions of compensation strength of the Lombard effect, recent comparative studies have begun to tackle new questions, including its phylogenetic origin [22–27], ontogeny [28–31], and circuit-level mechanisms that underlie it [3,5,32–34].

One of the fundamental questions concerning the Lombard effect, at least in mammalian species, pertains to the relative contribution of cortical and subcortical processes. At present,

**Highlights**

The Lombard effect is a phylogenetically ancient audiovocal phenomenon that may have emerged ~450 million years ago.

The Lombard effect is elicited by a subcortical network that processes acoustic features of stimuli, such as amplitude, frequency, and duration.

The Lombard effect is better explained by the SNR between a subject's vocalization and ambient noise, than by the amplitude of ambient noise *per se*. The physiological SNR of the auditory system is influenced by various parameters such as amplitude, call frequency, and duration, and Lombard effect for a given vocalization is determined by these parameters collectively.

Cortical networks can play a modulatory role in the Lombard effect, and may differentially influence the Lombard effect across groups of animals that differ with respect to neuroanatomical structure and organization.

The Lombard effect serves as a valuable behavioral paradigm to unravel the neural underpinnings of audiovocal integration, which is essential to many other aspects of vocal control.

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there is mixed evidence regarding the relative contributions of the two. On the one hand, there are compelling data suggesting that cortical processes participate in the Lombard effect. For example, the compensation strength of the Lombard effect in humans is influenced by communication tasks [35] and the Lombard effect in humans can be inhibited after training [36]. On the other hand, findings from animal studies – for instance, decerebrate cats exhibit the Lombard effect [32] – indicate that subcortical processes are sufficient to mediate the Lombard effect. Bats can initiate the Lombard effect with a response latency as short as 30 ms relative to noise onset [5], which implies that subcortical processes suffice in mediating adjustments in call level in response to background noise.

Here, we provide a framework to account for the Lombard effect, which reconciles data from humans and other animals. We propose that the Lombard effect is elicited by a subcortical network, which can be modulated by cortical brain areas in mammals or homologous higher level brain structures in vertebrates, such as the pallium in birds [37]. The proposed framework offers mechanistic explanations for two intriguing features of the Lombard effect: the widespread taxonomic distribution [17] and apparent variation in the compensation magnitude [38].

### The Lombard Effect Is Elicited by Subcortical Processes

The first line of evidence that subcortical processes suffice in eliciting the Lombard effect comes from the widespread taxonomic distribution of animals that adjust vocal amplitude in response to background noise, including species that lack cortical brain regions or the equivalent. Apart from humans, the Lombard effect appears in diverse animal groups of vertebrates, with empirical evidence from fish [24], frogs [25,26], birds [21,39–44], whales [45–48], cats [32], bats [3,4,49–52], and primates [9,12,53–56]. Species that were experimentally tested but did not show the Lombard effect include a frog [22], a gecko [27], and a manatee [57] (for details see below). Mapping the Lombard effect onto a **phylogenetic tree** of vertebrates [58–60], reveals that the Lombard effect is an evolutionally old behavior that may have emerged ~450 million years ago (Figure 1). From a neurobiological perspective, the widespread taxonomic distribution of species showing the Lombard effect is intriguing, because both the sound production and hearing systems across these animal groups are remarkably different. Mammals, including humans, produce vocalizations through the larynx, and the auditory system includes both subcortical and cortical structures. In nonmammalian species, the hearing and acoustic signal production systems vary and may differ substantially from those of mammals. As one example, the black bladder fish, which was found to show the Lombard effect [24], generates sound by drumming the sonic muscles of the swim bladder [61]. It is also important to note that the auditory pathway of fish includes brainstem and midbrain nuclei, projecting to the homolog of the thalamus in mammals, but lacks cortical structures [62,63].

The early developmental origin of the Lombard effect provides a second line of evidence that experience-driven cortical processes might not be involved in eliciting this behavior. The Lombard effect was observed in 2-day-old ducklings [31], 5-day-old infant bats [30], and 9-day-old tree swallows [29]. In humans, the youngest children tested explicitly for the Lombard effect were aged 3–4 years [28]. It is worth noting that a study of human infants showed that those aged 1 month cried louder when other infants were crying at the same time [64], suggesting that **audiovocal integration** brain circuits are operating at this early age, and that humans might show early developmental onset of the Lombard effect. These findings also suggest that the Lombard effect could be an innate capacity that does not require vocal learning. Innate or unlearned motor behaviors are generally controlled by subcortical processes, although cortical processes can play a modulatory role [65,66]. Of note, the neural substrates essential for vocal learning are located in cortical regions, such as the motor cortex

### Glossary

**Audiovocal integration:** interactive influences between auditory processing and vocal production control.

**Auditory feedback:** auditory monitoring of an organism of its own vocalizations during sound production.

**Lombard effect:** rise in call amplitude in an animal in response to increasing ambient noise level.

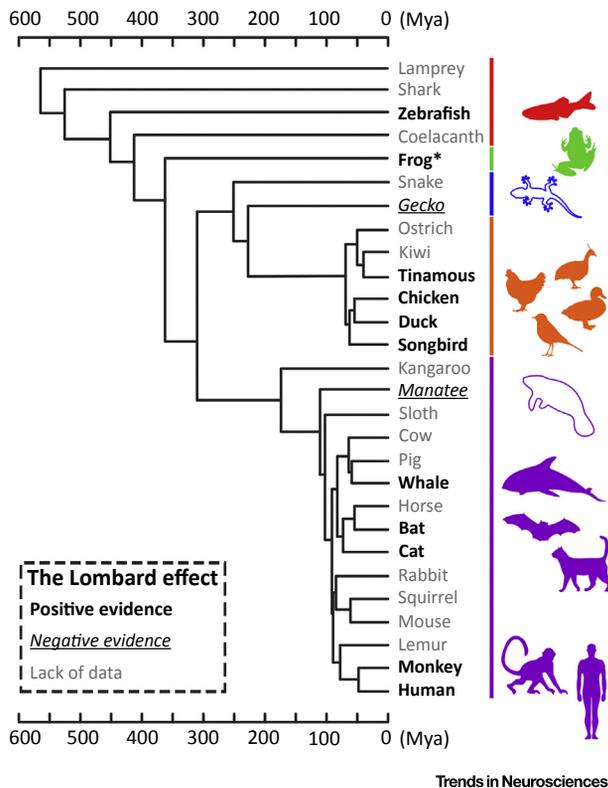
**Phylogenetic tree:** branching diagram showing the evolutionary relationship of species or taxa based on similarities in physical or genetic traits.

**Psychoacoustics:** research method that quantifies the relationship between acoustic signals and animal or human perception.

**Signal-to-noise ratio (SNR):** ratio between a signal and the background noise level; the physiological SNR refers to the relationship between signals and noise processed by the central nervous system.

**Speech intelligibility:** measure of the difficulty of understanding the speech, for example, in a quiet versus a noisy environment.

**Temporal summation:** refers to the integration of information over time. In the case of auditory signal detection, temporal summation of sound energy contributes to detection threshold.



**Figure 1. Phylogenetic Tree of the Lombard Effect.** The phylogenetic tree is modified from [58–60], showing selective groups of vertebrates. The species for which the Lombard effect was tested experimentally was mapped into the closest group of animals on which the phylogenetic tree was built. Red species: representatives of fish (Pisces); green: amphibians (Amphibia); blue: reptiles (Reptilia); orange: birds (Aves); purple: mammals (Mammalia); Mya, millions of years ago. The asterisk marks the species for which there is both positive and negative evidence for the Lombard effect.

and prefrontal cortex of humans [67] or their homologs, such as the robust nucleus of the arcopallium (RA) and HVC of songbirds [68].

A third line of evidence that subcortical processes suffice for the Lombard effect relates to the issue of response latency and comes from echolocating big brown bats (*Eptesicus fuscus*). Taking advantage of the brief-duration sonar calls of big brown bats, Luo *et al.* [5] studied the time course of the Lombard effect on a millisecond scale. Surprisingly, it took as little as 30 ms for the bats to increase the amplitude of their calls after noise onset. This rapid vocal–motor reaction time to auditory inputs suggests that the Lombard effect involves a limited number of synapses and thus can be initiated without the participation of cortical regions. Moreover, a simple model that builds on subcortical auditory processes alone can accurately capture and predict the fine time course of the Lombard effect in the echolocating bat. Of note, other studies have measured a longer response latency for the Lombard effect using a statistical approach, reporting a latency of ~300 ms for a bird [44] and ~100 ms for humans (K.R.A. Foery, MSc thesis, University of Colorado at Boulder, 2008). As we previously pointed out [5], a statistical approach by nature can yield an overestimation of the response latency. Specifically, the response latency of the Lombard effect in bats based on a statistical approach was ~75 ms, despite the fact that the bats were tested in a highly repeatable behavioral paradigm after training, which is far longer than the 30 ms based on the computational model fitting to the empirical data.

Collectively, the presence of the Lombard effect in fish and frogs without cortical structures, in neonatal birds and mammals, in decerebrate cats, and the short response latency demonstrated in echolocating bats, suggest that the subcortical network is sufficient to elicit the Lombard effect.

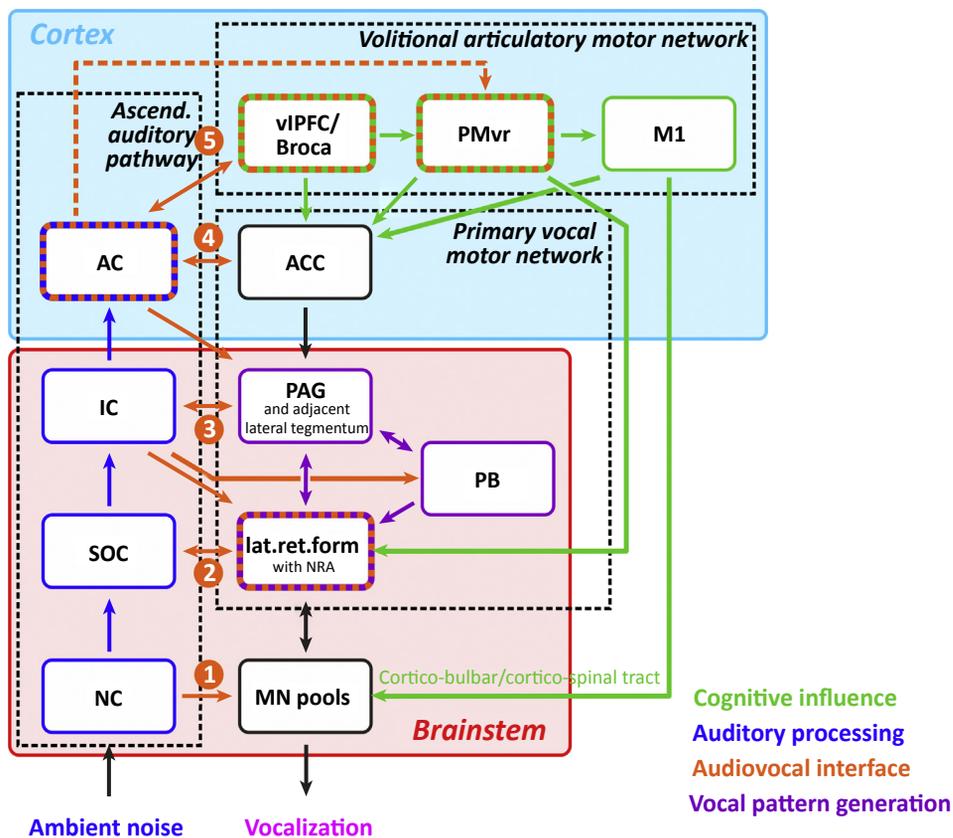
### Auditory Processing by Subcortical Processes

The first acoustic parameter implicated in the Lombard effect is the amplitude of ambient noise, which is central to the definition of the Lombard effect [16,17]. However, rather than the amplitude of ambient noise *per se*, growing evidence shows that the Lombard effect is better explained by the **signal-to-noise ratio (SNR)** between a subject's vocalization and ambient noise, and is more likely to occur under low-SNR conditions. For example, Luo *et al.* [30] studied the Lombard effect in young, pale spear-nosed bats, *Phyllostomus discolor*, which emit both sonar calls and social calls when they are separated from their mothers. The social calls were approximately 20–30 dB more intense than the sonar calls. At a moderate background noise amplitude of 52 dB SPL, the young bats increased the amplitude of the short sonar calls on average by 4.5 dB. By contrast, there was no sign of the Lombard effect on amplitude control of the social calls, which are produced at high SNRs.

We emphasize that SNR represents a crucial physical parameter in accounting for variation in the Lombard effect and bears relevance to the interpretation of the few instances in which certain species fail to show the Lombard effect. For example, the first experimental test of the Lombard effect in frogs (*Hyla chrysoscelis*) failed to reveal a Lombard effect [22], which led to the hypothesis that the Lombard effect is limited to birds and mammals [16]. Recently, two species of frogs (*Odorrana tormota* and *Physalaemus pustulosus*), studied independently by two groups of researchers, have provided strong evidence for the Lombard effect in anurans [25,26]. A close examination of this research revealed that the two studies reporting evidence for the Lombard effect tested frogs at lower SNR conditions (–5 to –20 dB), whereas the study that failed to show the Lombard effect tested frogs at SNR +20 dB. Similarly, the SNR hypothesis may also explain the absence of the Lombard effect in geckos (*Gekko gecko*) [27] and in the sea mammal manatee (*Trichechus manatus*) [57]. However, it is worth emphasizing that there are other explanations for the absence of the Lombard effect in some animals, including the observation that even in a silent environment, some species vocalize at high intensities, sometimes at the limit of their physical ability, and therefore cannot increase the amplitude of their calls further [27], or that some species rely on other vocal adjustment strategies, such as increasing the call rate or duration, to increase detectability in noise [22,27].

Computing the physical SNR between a vocalization and ambient noise is straightforward, yet the physiological SNR of the auditory system involves many processes. There are at least two acoustic parameters – call frequency and duration – both of which are processed by the auditory system and influence the physiological SNR. In other words, the Lombard effect for a given vocalization is determined by the frequency, duration, and amplitude of the ambient noise. The Lombard effect is most effectively evoked by noise that shares spectral components with the vocalization, and least effectively by noise whose spectrum does not overlap that of the vocalization. This finding is supported by data from birds [40,41], bats [3,49,50], monkeys [49], and humans [69,70].

The impact of noise duration on the Lombard effect has been investigated only recently. Luo *et al.* [5] showed that the Lombard effect in the big brown bat continued to increase with increasing noise duration up to ~300 ms. For noise durations of ≤50 ms, there was no clear evidence for the Lombard effect. Moreover, the same study revealed that the noise duration affects the Lombard effect through **temporal summation**, which is a conserved feature of the vertebrate auditory system. In **psychoacoustic studies**, it has been demonstrated, that for



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**Figure 2. Schematic Network Model for the Lombard Effect.** Simplified circuit diagram summarizing the most relevant structures for vocal production, auditory processing, and audiovocal interfaces. Arrows indicate anatomically verified and relevant direct connections. The brainstem structures of the primary vocal motor network (indicated in light red) generate vocal patterns, whereas the volitional articulatory motor network (indicated in light green) and the auditory network are capable of modulating vocal production. Audiovocal integration, indicated in orange, is happening on both subcortical (connections 1–3) and cortical level (connections 4 and 5). The neural network for vocal production is adapted from [67]. Abbreviations: AC, auditory cortex; ACC, anterior cingulate cortex; IC, inferior colliculus; LRF, lateral reticular formation; M1, ventral primary motor cortex; MN pools, motorneuron pools involved in vocal production; NC, cochlear nucleus; NRA, nucleus retroambiguus; PAG periaqueductal grey; PB, parabrachial nucleus; PMvr, ventrorostral premotor cortex; SOC, superior olivary complex; viPFC, ventrolateral prefrontal cortex.

short sounds, up to ~300 ms, detection threshold decreases with increasing sound duration [71,72]. Spiking activity in auditory nerve fibers shows a trading relationship between sound duration and amplitude, suggesting that psychoacoustic temporal summation builds on peripheral mechanisms [73,74].

### Possible Neural Substrates Underlying Subcortical Processing in the Lombard Effect

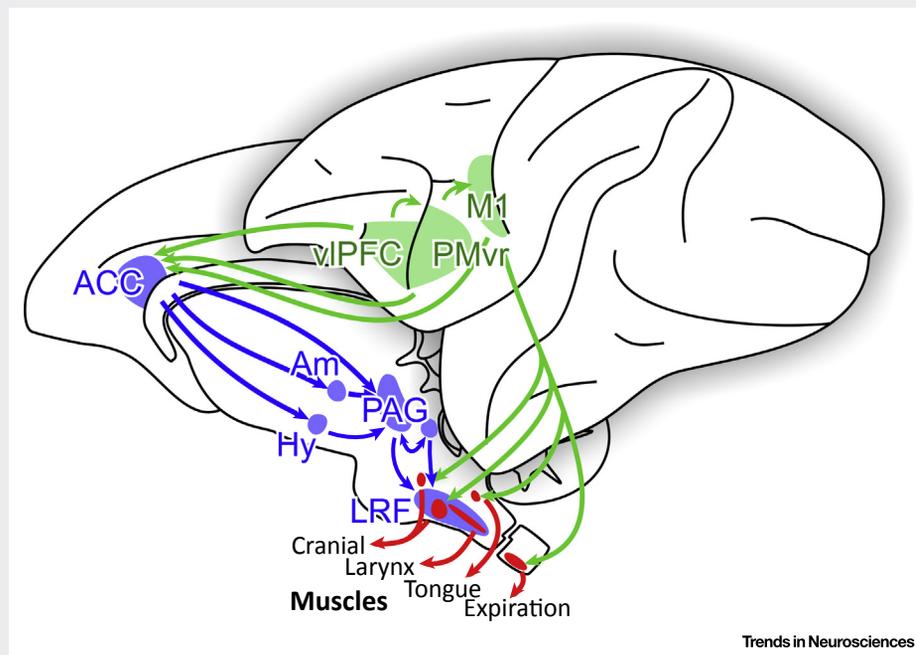
The short latency at which the Lombard effect is elicited [3,5] suggests that auditory activity early in the ascending auditory pathway feeds back onto the primary vocal motor network (Figure 2; Box 1). Previous studies identified a vocal-pattern-generating network in the brainstem, containing structures, such as the periaqueductal grey (PAG), the parabrachial nucleus, and the lateral reticular formation of the lower brainstem [67,75,76]. Based on the current literature, there are three anatomically and physiologically verified circuits that are capable of mediating audiovocal integration processes between the vocal motor system and the auditory projections to the

### Box 1. Neural Network Model for Vocal–Motor Control in Mammals

Recently, a dual neural network model was suggested that postulates two structurally and functionally distinct circuits for vocal–motor control [67], a volitional articulatory motor network (VAMN) originating in the ventrolateral portion of the prefrontal cortex (vIPFC), which controls the vocal output of a phylogenetically conserved primary vocal motor network (PVMN), mainly situated in subcortical structures.

All mammals possess a PVMN that produces species-specific vocalizations [75]. This PVMN consists of two structurally and functionally distinct parts. (i) A highly conserved vocal pattern-generating system in the brainstem, which consists of the PAG and the lateral reticular formation of the lower brainstem and bordering medulla. The PVMN coordinates all muscles involved in vocal production. (ii) An upstream limbic vocal-initiating network including structures such as the anterior cingulate cortex, amygdala, and hypothalamus, which drive a vocal pattern generator influenced by affective states (Figure 1) [67,75,76]. Recent studies have indicated that in nonhuman primates, a cortical network, including vIPFC as well as the premotor and primary motor cortices, is involved in cognitive control over the PVMN during vocal–motor production. Single neurons in the monkey prefrontal cortex predict the preparation of instructed vocalizations, suggesting a putative homolog of the human Broca’s area (area 44 and 45) [106]. The human Broca’s area is a crucial structure involved in the coordination of motor commands for speech initiation.

To our knowledge, it is not yet known whether vertebrates other than primates possess a cognitive network comparable to the primate VAMN that is capable of influencing the PVMN during call production. However, the evolutionary theory postulates preadaptations of the VAMN beyond the primate lineage, no matter how exiguous they might be [107]. In addition, the fact that vocal flexibility exists in birds and nonprimate mammals, such as bats [108,109], predicts neural networks that are capable of cognitive modulation of vocal output in these species. We suggest that distinct characteristics of the Lombard effect, such as its flexibility within a specific animal species, might be a good indicator of a potential modulatory effect of higher order structures on vocal motor output.



**Figure 1. Dual-Network Model for Vocal–Motor Production.** Structures and connections of the VAMN are indicated in green and of the PVMN in blue. Adapted from [67]. Abbreviations: ACC, anterior cingulate cortex; Am, amygdala; Hy, hypothalamus; LRF, lateral reticular formation; M1, ventral primary motor cortex; PAG, periaqueductal grey; PMvr, ventrorostral premotor cortex; PVMN, primary vocal motor network; VAMN, volitional articulatory motor network; vIPFC, ventrolateral prefrontal cortex.

brainstem, spanning from the midbrain to the medulla. The first connection is the direct projection from the cochlear nucleus to the laryngeal and respiratory motor neuron pools involved in vocal

production (Figure 2). This connection seems to be solely responsible for the laryngeal reflex; a rapid reflexive activation of the recurrent laryngeal nerve in response to external acoustical stimulation (minimum latency: 6 ms in bats [77] and 11 ms in humans [78]). However, it seems unlikely that the laryngeal reflex is involved in the initiation of the Lombard effect since the sound levels required to elicit this reflex ( $>50$  dB SPL [77]) are higher than the sound amplitudes required to elicit the Lombard effect [5,9,50,79]. Additionally, the Lombard effect exhibits longer response latencies ( $\sim 30$  ms in a bat [5] and 90–176 ms in humans; K.R.A. Foery, PhD thesis, University of Colorado at Boulder, 2008) than those reported for the laryngeal reflex.

Two more connections between the primary vocal motor network and the primary auditory pathway can be found. One is at lower brainstem levels between the superior olivary complex and the lateral reticular formation, encompassing the vocal pattern generator [80,81], and the other is at the pontine brainstem level between the inferior colliculus (IC) and the PAG [80,81] (Figure 2). Additionally, IC shows direct connections to the candidate audiovocal hub in the lateral reticular formation, which contains single neurons that respond to external acoustical stimuli and also show changes in neural activity prior to and during vocal production [33]. Based on the current literature, we suggest that the Lombard effect is implemented at subcortical levels, with the lateral reticular formation and PAG as possible audiovocal hubs in the primary vocal motor network. However, further neurophysiological studies are required to identify the locus of specific neural circuits mediating the Lombard effect.

### The Lombard Effect Can Be Modulated by Cortical Processes

Early evidence that cortical processes can modulate the Lombard effect comes from the observation that in humans, the Lombard effect can be influenced by communication tasks [20]. In an experiment that directly tested this hypothesis, Garnier *et al.* found that humans exhibited a stronger Lombard effect when they were involved in an interactive communication task than in a noninteractive reading task [35]. The impact of communication tasks on the Lombard effect is generally interpreted as evidence that the Lombard effect serves to increase communication efficiency or **speech intelligibility** [20,38,82,83]. In line with this interpretation, one recent study found that the Lombard effect was much stronger in a communication setting in which humans were not in visual contact and relied entirely on acoustic signals [84].

Another line of evidence for the modulatory role of cortical processes in the Lombard effect comes from experiments that involved training humans to inhibit the Lombard effect. Specifically, the Lombard effect in humans was substantially reduced or even blocked when humans were trained to maintain their vocal level in noise through visual feedback displaying their instant vocal level [36,85]. The effect of training on the Lombard effect stands out in professional choral singers, who show a weaker Lombard effect than nonprofessionals show [86,87]. Moreover, there is evidence that the extent to which the Lombard effect can be reduced is influenced by the cognitive capacity of humans. Specifically, a study found that humans who performed writing tasks requiring more cognitive resources suppressed the Lombard effect to a lesser extent than those who performed writing tasks requiring fewer cognitive resources [88].

### Cognitive Influences on the Lombard Effect May Not Be Restricted to Humans

Some data suggest that the Lombard effect in diverse animal species might also be modulated by cognitive processes. Kobayasi and Okanoya found that Bengalese finches exhibited the Lombard effect when producing undirected but not directed songs [89]. In that study, the apparent difference in the Lombard effect could not be simply explained by the acoustic differences between the song types, and these authors suggested that social context may have

played a role. More recently, Luo *et al.* tracked the Lombard effect in adult pale spear-nosed bats over 3 months and found that the Lombard effect became gradually weaker [30]. This finding suggests that the Lombard effect is modulated by sensory experience, and possibly through habituation [90,91]. Future studies are needed to investigate the causal role of cognitive influences on the Lombard effect in other animal species.

### Possible Neural Substrates Underlying the Cognitive Influences

Neurophysiological investigations of cortical influences on the Lombard effect are rather limited. To our knowledge, the only neurophysiological investigation that examined potential modulatory influences on the Lombard effect at the cortical level comes from Eliades and Wang. Combining sound recordings of vocalizations and extracellular recording from neurons in the primary auditory cortex of marmoset monkeys, the authors reported that masking noise increased the firing rate of a population of neurons. More importantly, they found that the change in firing rate of the neurons between noise and silence predicted the magnitude of the Lombard effect [55]. In humans, various behavioral experiments suggest that the Lombard effect is potentially under modulatory influences by large cortical networks (Figure 2) and their related sensorimotor systems, including visual [36,85], primary motor [92], somatosensory [85], and prefrontal [93] cortices. For example, researchers found that instruction alone was not enough for humans to resist the Lombard effect, which can be largely inhibited when humans are provided with visual feedback of their vocal level [36], illustrating an influence of visual information processing on the Lombard effect. Going forward, it will be essential to confirm the causal role of potential candidate cortical regions in eliciting short-term modulatory effects on the Lombard effect.

We suggest that the prefrontal cortex is a candidate region for modulatory influences on the Lombard effect, based on current research in nonhuman primates. The primate prefrontal cortex is involved in a variety of executive functions, such as vocal motor control [94]. The prefrontal cortex serves as a hub for sensorimotor integration involving multiple modalities, including vision, hearing, and somatosensation [67,95]. The prefrontal cortex is interconnected with several auditory areas within higher-order structures of the auditory cortex [96–98]. A recent study showed that audiovocal neurons in the ventrolateral portion of the prefrontal cortex in monkeys are involved in complex audiovocal integration processes [99]. Thus, in primates an anatomically and physiologically plausible circuit, capable of modulating the Lombard effect, projects from the auditory to ventrolateral prefrontal cortex, to the ventrorostral premotor cortex (PMvr), and to the pontine reticular formation [80], with all areas serving as potential hubs of audiovocal integration and modulation [34,99–101]. Since the PMvr is directly connected to the vocal-pattern-generating network in the brainstem and to the premotor neurons involved in phonation [102,103], it might also directly modulate ongoing vocalizations in response to external acoustic events. In line with this suggestion, recent work reported that external acoustic events are capable of rapidly modulating ongoing vocalizations in marmoset monkeys [15].

We propose that cognitive control over the Lombard effect in distinct model species depends on the relative size of the prefrontal cortex [104] and the strength of its interconnections with other cortical and subcortical brain structures. Specifically, we predict that animals with a relatively large prefrontal cortex and strong auditory connections to this brain region, such as bats and nonhuman primates [105,106], are more likely to exhibit cognitive modulation of the Lombard effect, similar to humans. By contrast, animals exhibiting the Lombard effect, but lacking homologs or analogs of mammalian prefrontal lobe structures, such as fish and frogs, would show a rather inflexible and stereotyped expression of the Lombard effect.

## Concluding Remarks

Recent research on the Lombard effect has dramatically changed scientific views on this audiovocal behavior. Key to this progress are comparative studies using a variety of animal models, which have demonstrated that the Lombard effect is widespread across the phylogenetic tree of vertebrates. Apart from the fact that the amplitude of vocalizations can be directly quantified, both in the laboratory and in the field, the widespread taxonomic distribution of animals showing the Lombard effect makes it readily accessible for cross-species comparisons across environmental and behavioral contexts. Moreover, the Lombard effect presents a fruitful behavioral paradigm for investigating the neurophysiological

### Box 2. Computational Processes of Sensorimotor Integration

Sensing and motor control are two intermingled processes underlying natural behaviors, from reaching for a coffee mug to producing intelligible speech. Although the behavior of reaching for a coffee mug differs along many dimensions from producing intelligible speech, knowledge gained from one form of motor control can benefit scientific advances in another. Particularly, diverse sensorimotor behaviors in both humans and animals may share common computational processes that can be explained by the state feedback control (SFC) model [110–113].

This SFC model (Figure 1) posits that sensorimotor systems issue commands to activate muscle groups, which result in behaviors, such as moving the hand to reach for a coffee mug or the larynx to produce speech. In both examples, the motor system predicts the sensory consequences of the motor commands based on an internal model, a process termed forward prediction. The predicted sensory consequences are combined with direct sensory feedback through a process termed state estimation, which is then used to update motor commands. In addition to receiving the sensory feedback from the self-generated action, sensory systems also process external sensory inputs from the environment. Since the sensory feedback is delayed, and the external sensory environment can be noisy, motor control is achieved primarily through forward prediction, whereas actual sensory feedback is used to train and update the internal model [111].

A key problem in motor control research is the role of sensory feedback. The contribution of auditory feedback to the Lombard effect is still under debate. On the one hand, there is direct evidence that the Lombard effect does not necessarily require sensory feedback. Hage *et al.* found that the greater horseshoe bats showed the Lombard effect in the first call after noise onset, indicating that the bats did not use auditory feedback to increase the amplitude of their vocalizations [3]. On the other hand, it is well documented that the Lombard effect depends on spectral overlap between vocalization and background noise [40,49,70]. Auditory feedback might be used to extract the spectral information of ongoing vocalizations and compare it with the background noise.

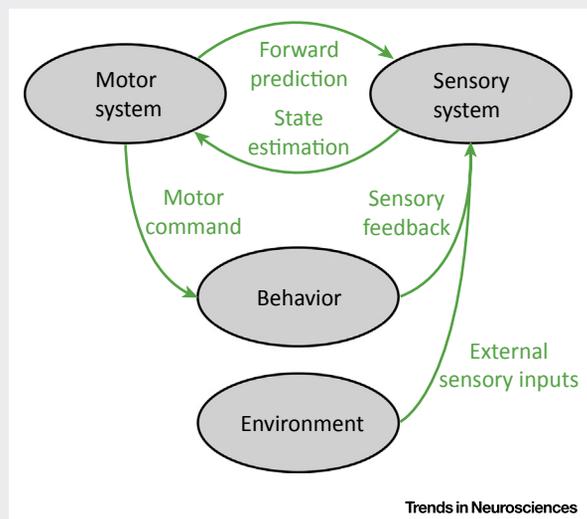


Figure 1. A Highly Simplified View of Motor Control. Modified from [110,111,113].

## Outstanding Questions

What specific neural circuits within the primary vocal motor network underlie the Lombard effect?

Do the neural circuits of the Lombard effect overlap with the neural circuits for other forms of audiovocal integration, for instance pitch control?

How do cognitive influences on the Lombard effect differ across species, including humans? In particular, can animals deliberately inhibit the expression of the Lombard effect, as shown in humans?

What mechanisms drive developmental changes in the Lombard effect?

basis of audiovocal integration throughout the animal kingdom. In addition, the Lombard effect is both reflexive and influenced by cognitive processes in some species, which presents opportunities to study the underlying neural circuits at both subcortical and cortical levels. Lastly and more broadly, we assert that researchers investigating different sensorimotor behaviors can mutually benefit from sharing methods, data, and interpretations. As highlighted in **Box 2**, various sensorimotor behaviors share similar computational processes. Comparative and integrative research can serve to delineate the common and distinct brain regions and/or circuits responsible for diverse sensorimotor behaviors, ranging from the Lombard effect to reaching and grasping (see Outstanding Questions).

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