into its own redox chemistry and use it to reduce external solid minerals, just as *Shewanella* does (Proc. Natl. Acad. Sci. USA (2010), *107*, 19213–19218).

## Back to the beginning

Apart from the desire to make life a little bit different from the version that already exists and from the view that you can only understand things if you can make them, there is a third, independent reason for scientists to try their hands at synthetic biology, namely the attempt to figure out how life originated in the first place.

The ultimate in synthetic biology would be to be able to start from small molecules and synthesize a living, reproducing, evolving entity from scratch. Our understanding of prebiotic chemistry, and everything that then happened until the advent of the last common ancestor of today's species, is still far too incomplete to allow researchers the slightest hope of achieving such a feat. Yet the synthetic biology community also includes researchers who try to reconstruct certain stages on the path towards life.

For instance, Aniela Wochner from the MRC Laboratory of Molecular Biology at Cambridge, presented work on "reconstructing the RNA world" at the SB5.0 meeting. Using *in vitro* evolution techniques, her work involves engineering ribozymes that can polymerise RNA, a key requirement for a self-sufficient RNA world (see also Science (2011), *332*, 209–212).

Beyond the design of futuristic new life, Steven Benner is also interested in the recreation of early life. Thus, parts of his research efforts are directed towards 'paleogenetics', i.e. the extrapolation of the genes of long-forgotten common ancestors, and the expression of the proteins corresponding to these genes. With this approach, Benner's group has addressed questions such as the thermophilic tendencies of early bacteria and the biochemistry of ruminant digestion.

In creating new life and recreating how life came to be here, while tackling unsolved mysteries around its functional mechanisms, it sounds as though synthetic biology, taking over from the classic 20<sup>th</sup> century reductionist and analytical approach, has enough work to do for the rest of this century.

Michael Gross is a science writer based at Oxford. He can be contacted via his web page at www.michaelgross.co.uk

## **Quick guides**

## **The Lombard effect**

Sue Anne Zollinger and Henrik Brumm

What is it? This year marks the 100 year anniversary of the discovery of the Lombard effect, an involuntary vocal response by speakers to the presence of background noise. In the century since its discovery, this phenomenon has surely achieved importance far beyond what its discoverer could have ever imagined. In the simplest terms, the Lombard effect is an increase in vocal amplitude in response to an increase in background noise. Although most people are probably not aware of it, we all know the Lombard effect just think of the last time you tried to engage in a conversation in a noisy pub or at a boisterous party (Figure 1).

How did it get its name? In 1911, a French otolaryngologist named Étienne Lombard published an article entitled "Le signe de l'élévation de la voix", which described an interesting observation he made while working at the Hôpital Lariboisière in Paris (Figure 2). Lombard had noticed that when a patient who was engaged in conversation was presented with an intense noise, he would elevate the level of his speaking voice. Lombard perceived that the patient did not seem aware of this change in vocal amplitude, and concluded this was an involuntary reflex: he thought that this "sign of the elevation of the voice" could be used as a tool to ferret out malingerers pretending to be deaf in order to shirk their work duties, or make false claims of injury.

The discovery was dubbed the 'Lombard sign' by Lombard's student in a subsequent publication and the terminology was soon adopted by others. Because of the involuntary nature of the phenomenon, some authors began using the term 'Lombard reflex'. Both names are still sometimes used, but as the phenomenon is not a true reflex the most common and generally accepted term is the 'Lombard effect'. How does it work? Although the adjustment of vocal intensity happens involuntarily when background noise levels change, the phenomenon is not truly a reflex. Much of what we do know about how the Lombard effect works at a neural level comes from comparative work on non-human primates and other mammals. From these studies we learn that the essential circuits responsible for the Lombard effect are located in the brainstem. Specifically, sets of audio-vocal neurons in the periolivary region and the pontine reticular formation are the most likely candidates for the integration of vocal production and auditory perception that is necessary for the Lombard effect.

As mentioned above, however, the Lombard effect is not a true reflex, in that it is not controlled by a simple reflex arc. One clue that higher cortical areas are involved is that the effect, although involuntary, can be modulated by social context and can be inhibited with training involving feedback from a different sensory modality. Although the Lombard effect is robust and simply instructing speakers to keep their voice level constant does little to inhibit it, when speakers are provided with visual feedback displaving their vocal intensity in real time, it is possible to train a speaker to inhibit the rise in voice amplitude.

While the term 'Lombard effect' generally describes only the change in vocal amplitude, the effect is very often accompanied by a suite of other vocal changes, including a rise in fundamental frequency, a



Figure 1. The Lombard effect.

Even if you weren't aware of the Lombard effect, or what it was called, you almost certainly exhibited it the last time you had a conversation in a noisy club, at a loud party or on a busy street corner with a car or bus passing by. (Photograph courtesy of Damon Locks.) flattening of spectral slope (or 'tilt'), and an elongation of signal duration. This collection of related vocal adjustments in response to noise is collectively referred to as 'Lombard speech' in humans.

The degree to which these other traits are coupled to the rise in amplitude can depend on the type and context of the vocalization. For example, in human speech, vowels are more likely to be elongated in Lombard speech, while consonants usually are not. In humans, males tend to exhibit a more dramatic Lombard effect than females do, and speakers in general have stronger Lombard effect-related vocal changes when they are involved in communicative interactions than when they are simply reading or speaking in a non-communicative context. Interestingly, these changes in voice parameters observed during Lombard speech differ from those that occur during voluntary 'loud speech', as when a speaker is simply asked to talk louder or when a teacher raises her voice to address students in a large lecture hall. This finding further emphasizes the reflexlike nature of the Lombard effect, and may be an indication that different neural control mechanisms are involved in voluntary vs. involuntary changes in voice amplitude.

Why is it important? In addition to its usefulness in diagnosing hearing loss (or someone faking it), Lombard himself recognized that his 'sign' had other potential applications. He recognized that the Lombard effect was the result of a feedback system between vocal production and auditory perception that enabled correction of speech performance. The Lombard effect is still widely used in hearing tests and in studies of audio-vocal integration. The Lombard effect is also applicable to the study of vocal disorders and speech production, and has even been used as a therapeutic tool to improve speech intelligibility in Parkinson's disease patients.

Beyond the medical and psychobiological applications mentioned above, the Lombard effect has proved relevant across a diverse range of other fields. Understanding the Lombard effect, and particularly the changes associated with Lombard speech, has been instrumental in developing software for automatic speech and speaker recognition. In architectural acoustics and design, studies on the Lombard effect are employed to reduce unwanted noise and improve intelligibility of speech indoors. The Lombard effect is also relevant to the study of phonetics and linguistics.

During the last decades, the Lombard effect has become increasingly important in the study of animal vocal behaviour and of the evolution of vocal plasticity. The Lombard effect has been demonstrated experimentally in a range of other mammals, including non-human primates, cats, bats and whales. In birds, the Lombard effect has been experimentally shown in a diverse set of taxa, ranging from chickens to songbirds. A recent study, however, could not find evidence for this faculty in frogs, suggesting that the Lombard effect is not a common trait of all vertebrates. Whether or not the effect has evolved independently in birds and mammals is not known to date but future research may close this gap.

How can researchers use it in their future work? The number of research articles referencing the Lombard effect has grown steadily in the 100 years since Étienne Lombard first published his findings. The Lombard effect is now understood to be more than just a simple raising of the voice, but is a complex array of dynamic vocal changes in response to realtime changes in the perception and production of one's own voice, and to changing environmental acoustic and social conditions. That the Lombard effect is often, but not always, accompanied by spectral and temporal changes in the vocal signal suggests that these traits are not simply coupled biomechanically, but to some degree are capable of independent modulation.

The importance of this vocal phenomenon in future research is increasingly broad. In recent years there has been a surge of interest in the negative effects of rising levels of anthropogenic noise on wildlife (and on humans). As a result, an understanding of the Lombard effect and of the mechanisms underlying and constraining



Figure 2. The Hôpital Lariboisière in Paris, France.

This is where Étienne Lombard discovered the noise-dependent regulation of speech amplitude 100 years ago. (Photograph courtesy of Ana Martins.)

vocal communication in noise is particularly relevant to today's scientific community.

We still know far too little about the neural mechanisms that mediate the Lombard effect, particularly when it comes to the differences between taxa. The examination and understanding of these mechanisms are not only relevant to human speech regulation, but would provide insight into the evolution of this vocal phenomenon.

## Where can I find out more?

- Brumm, H. and Slabbekoorn, H. (2005). Acoustic communication in noise. In Advances in the Study of Behavior, vol. 35. (San Diego: Elsevier Academic Press Inc.) pp. 151–209.
- Brumm, H., Schmidt, R., and Schrader, L. (2009). Noise-dependent vocal plasticity in domestic fowl. Anim. Behav. 78, 741–746.
- Garnier, M., Henrich, N., and Dubois, D. (2010). Influence of sound immersion and communicative interaction on the Lombard effect. J. Speech Lang. Hear. Res. 53, 588–608.
- Hage, S.R., and Jürgens, U.E.G. (2006). Audio-vocal interaction in the pontine brainstem during self-initiated vocalization in the squirrel monkey. Eur. J. Neurosci. 23, 3297–3308.
- Ho, A.K., Bradshaw, J.L., lansek, R., and Alfredson, R. (1999). Speech volume regulation in Parkinson's disease: effects of implicit cues and explicit instructions. Neuropsychologia 37, 1453–1460.
- Lane, H., and Tranel, B. (1971). The Lombard sign and the role of hearing in speech. J. Speech Hear. Res. 14, 677–709.
- Lombard, E. (1911). Le signe de l'élévation de la voix. Annales des Maladies de L'Oreille et du Larynx 37, 101–119.
- Love, É.K., and Bee, M.A. (2010). An experimental test of noise-dependent voice amplitude regulation in Cope's grey tree frog (Hyla chrysoscelis). Anim. Behav. 80, 509–515. Pick, J.H.L., Siegel, G.M., Fox, P.W., Garber,
- Pick, J.H.L., Slegel, G.M., FoX, P.W., Garber, S.R., and Kearney, J.K. (1989). Inhibiting the Lombard effect. J. Acoust. Soc. Am. 85, 894–900.

Communication and Social Behaviour Group, Max Planck Institute for Ornithology, 82319 Seewiesen, Germany. E-mail: zollinger@orn.mpg.de; brumm@orn.mpg.de