

Ultrasonic Hearing in Cats and Other Terrestrial Mammals

M. Charlotte Kruger, Carina J. Sabourin, Alexandra T. Levine, and Stephen G. Lomber

What is the first thought that comes to your mind when you read the word “ultrasound”? Most readers of *Acoustics Today* might associate ultrasound with pregnancy or perhaps specialized detection technology on ships and airplanes. Some might also think about echolocating animals. But what about terrestrial mammals? The ones that walk the earth among us? Although the use of ultrasound in echolocating mammals (e.g., bats, dolphins, and whales) is well-known, our understanding of ultrasonic perception in nonflying terrestrial mammals is limited. Here we discuss the frequencies perceived and the biological importance of ultrasound for four land-dwelling mammals as well as what is currently known about the various areas in the brain that allow these animals to process ultrasound.

What We Know About Ultrasound

Ultrasonic sounds differ from “regular” sounds because their frequencies are too high for humans to detect. The upper hearing limit for humans is considered to be 20 kHz, and sounds with a frequency above 20 kHz are considered ultrasonic. This is the agreed on definition, yet this distinction is subjectively based on the range that we, as humans, can hear and has no biological basis per se.

Despite not being able to hear ultrasound, humans often capitalize on its presence. The most familiar use would be clinical applications of ultrasound (e.g., Ketterling and Silverman, 2017). These include pregnancy scans, observation of pathology progression, and treatments such as the elimination of kidney stones (Simon et al., 2017). In industrial environments, ultrasound is used as a nondestructive test to measure the thickness and quality of objects. Even though ultrasound can be useful for humans in a variety of settings, public exposure to airborne ultrasound is suggested to also cause adverse effects, such as nausea, dizziness, and failure to concentrate (Leighton et al., 2020). However, this is not the case for many animals. Long before humans started utilizing ultrasonic frequencies, animals have been using ultrasound for various beneficial reasons.

Signals containing ultrasound play a pivotal role in the lives of many species. Well-known uses include prey detection, finding mates, and communicating with conspecifics. High frequencies have very short wavelengths and therefore attenuate more rapidly when traveling through air compared with lower frequencies. Therefore, ultrasonic production and hearing create a private communication channel that subverts detection by prey as

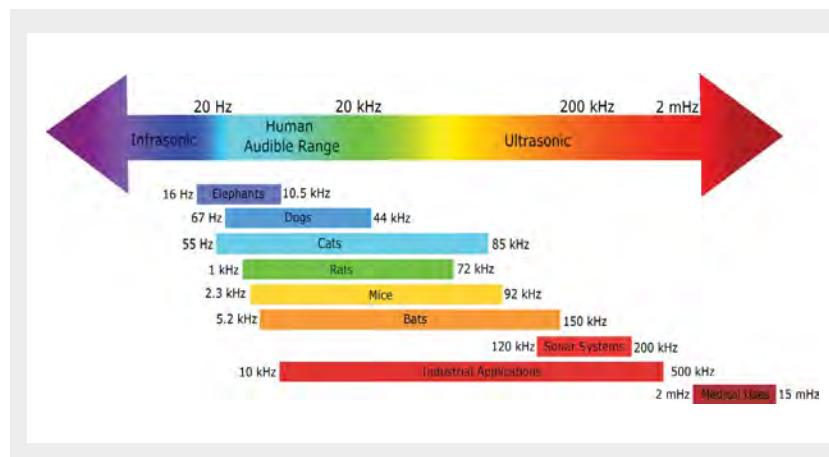


Figure 1. Frequencies for the hearing abilities of mice and rats (*Mus musculus* and *Sigmodon hispidus*, respectively; Masterson and Heffner, 1980), elephants (*Elephas maximus*; Heffner and Heffner, 1982), domestic cats (*Felis catus*; Heffner and Heffner, 1985), domestic dogs (*Canis lupus familiaris*; Heffner, 1983), and short-tailed fruit bats (*Carollia perspicillata*; Koay et al., 2003) at 60 dB sound pressure level (SPL) as well as familiar human applications of ultrasound (Jensen, 2007; Carovac et al., 2011; Harvey et al., 2014).

well as by predators that are unable to hear the higher frequencies (Ramsier et al., 2012). Examples of animals that can hear ultrasound include cats, dogs, bats, mice, and rats (Figure 1). Through technological advances, we have been able to detect, observe, study, and utilize these signals found outside our perceptual capabilities (Arch and Narins, 2008). By investigating different animals that can hear ultrasound, we better our understanding of the physiological and anatomical mechanisms behind their ability to perceive these high-frequency sounds.

The Auditory Pathway and Ultrasound

The auditory system provides animals with the ability to detect and perceive sounds over a wide range of frequencies and intensities. Sound waves travel through the outer and middle ear before being transferred to the cochlea in the inner ear. The cochlea deconstructs sounds of differing frequencies and intensities into electrical signals that can be interpreted by the brain. These electrical signals travel up the auditory pathway from the cochlea, passing through the brainstem, until eventually being relayed by the nuclei in the thalamus to their final destination, the auditory cortex.

Neurons in the auditory cortex are generally arranged according to the frequency at which they respond with the greatest sensitivity, namely their characteristic frequencies. In many animals, the characteristic frequencies of neurons progress linearly along the cortical surface as a tonotopic map (Moerel et al., 2014). This organization allows the identification of neurons responsible for conveying specific kinds of information such as ultrasound. As such, it is important to consider where these specific neurons for encoding ultrasonic frequencies are found within the cortices of terrestrial mammals and what the relevance and benefits associated with the ability to detect ultrasound might be.

Measuring the Audible Frequency Range

Audiometry experiments can provide insight into the ultrasonic abilities of different species. The point at which a sound is detected is known as the audibility threshold. As described in a previous issue of *Acoustics Today* (Dent, 2017), psychophysical approaches are often employed to measure perceptual thresholds in nonhuman species. Psychophysical approaches encapsulate experimental designs where a physical stimulus is presented to a subject and the neural and/or sensory responses evoked by the stimulus

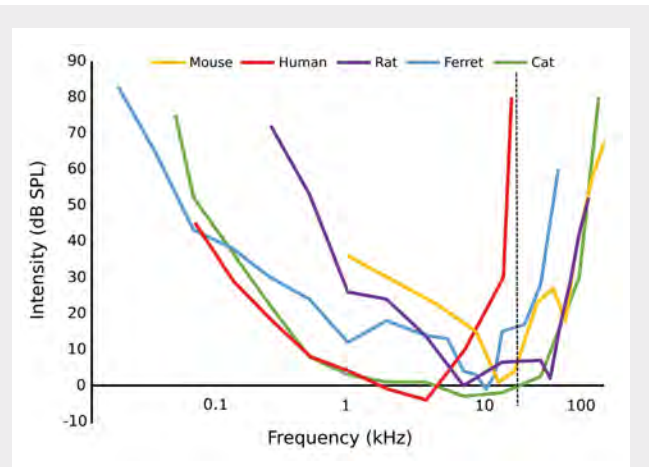


Figure 2. A behavioral audiogram for the mouse (*Mus musculus*; Ehret, 1974), ferret (*Mustela putorius furo*; Kelly et al., 1986), human (*Homo sapiens*; Sivian and White, 1933), rat (Kelly and Masterson, 1977), and cat (*Felis catus*; Heffner and Heffner, 1985). **Dashed vertical line**, beginning of the ultrasonic range (20 kHz). Data represent the lowest sound level detected at each frequency.

are examined. Psychoacoustics, one form of psychophysics, analyzes the relationship between auditory stimuli and neural events by employing various conditioning techniques (Dent, 2017). The results of the different conditions tested are often depicted using an audiogram (Figure 2).

Biological Importance

Rodents

Small rodents such as rats and mice emit and perceive ultrasonic sounds to communicate with conspecifics for a variety of social communicative interactions, including courtship and mating, aggression and territoriality, reproduction, and to alert conspecifics (Arch and Narins, 2008).

Male mice produce ultrasonic vocalizations between 48 and 79 kHz in response to female pheromones to attract them as a potential mate (Gourbal et al., 2004) and emit vocalizations up to 75 kHz when sniffing or mounting female mice (Matsumoto and Okanoya, 2016). Furthermore, mouse pups produce isolation calls with frequencies between 50 and 80 kHz when they are separated from their nest (Hofer et al., 2001). Because mice can hear frequencies between 1.5 and 92 kHz at 60 dB sound pressure level (SPL; Heffner et al., 2001), the pup vocalizations reliably elicit a retrieval response from the mothers (Dunlap and Liu, 2018). The frequencies used in courtship vocalizations

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produced by male mice to attract females shows the sex-specific relevance of ultrasound production and hearing.

Similar to mice, adult rats have two main purposes for emitting ultrasonic vocalizations as a form of communication: alarm calls at 22 kHz to warn conspecifics of danger and calls at 50 kHz for social cooperation and affiliative behavior (Wright et al., 2010). Rats generally emit vocalizations with frequencies that fall within their hearing range (between 250 Hz and 80 kHz). For example, infant rats can emit vocalizations between 40 and 65 kHz when they are separated from their nest, and adult rats can emit ultrasonic calls to solicit sexual behavior from the opposite sex (Portfors, 2007). On hearing the 50 kHz vocalizations from male rats, females display a series of attracting behaviors, increasing the likelihood of the male approaching and copulating (Portfors, 2007). Rodents therefore rely on ultrasound for their survival whether it is for communicating with conspecifics, attracting mates, or evading predators.

Carnivores

Unlike rodents, there are only limited data available on the evolution and biological importance of ultrasonic hearing in carnivores. Carnivores, aside from carnivorous rodents like the northern grasshopper mouse (*Onychomys leucogaster*), are seldom known to produce or use ultrasonic frequencies for communication (Brown et al. 1978; Farley et al., 1987). Even so, many carnivores can perceive sounds with ultrasonic frequencies. It is thought that perhaps, at one point in history, the common ancestor of carnivores used ultrasound for prey detection (Heffner and Heffner, 1985; Kelly et al., 1986). However, as discussed in *Rodents*, prey (such as mice or rats) primarily communicate at frequencies above the hearing range of carnivores (Kelly and Masterton, 1977).

Phillips and colleagues (1988) determined that ferrets (*Mustela putorius furo*) can detect sounds from 40 Hz to approximately 40 kHz. Ferrets provide a useful model for investigating the development, organization, and plasticity of the auditory cortex because the onset of hearing in ferrets occurs late compared with other mammals (Moore, 1982). Before their ear canals open, newborn ferrets, known as kits, produce high-frequency vocalizations often above 16 kHz. Lactating female ferrets respond to these kit vocalizations (Shimbo, 1992) similar to the rodent behavior described in *Rodents*. Overall, ferrets provide useful models for investigating different aspects of hearing and hearing loss, given that their hearing range largely overlaps that of humans (Fritz et al., 2007).

Another common carnivore model used for auditory research is the domestic cat (*felis catus*). The sensitive hearing range of cats is commonly believed to be between 5 and 32 kHz, although there are notable discrepancies in the literature regarding their hearing range limits (Figure 3). The literature agrees that cats can hear ultrasonic frequencies, but the full extent of their perception remains unclear. The lower limit of hearing is generally reported as approximately 125 Hz, but the upper limit is not well defined.

Most sources report the upper limit as the maximum frequency tested. As such, the upper hearing limit of cats is not commonly described as greater than 60 kHz (Figure 3), and, in some cases, the reported upper limit corresponds to the highest frequency of sound tested in the respective study. This is true for both electrical stimulation experiments, where electrical impulses are applied to neurons in the auditory pathway, and behavioral experiments. One exception is a study by Heffner and Heffner (1985) who tested frequencies up to 92 kHz and reported the upper hearing limit as 85 kHz. Therefore, it is possible

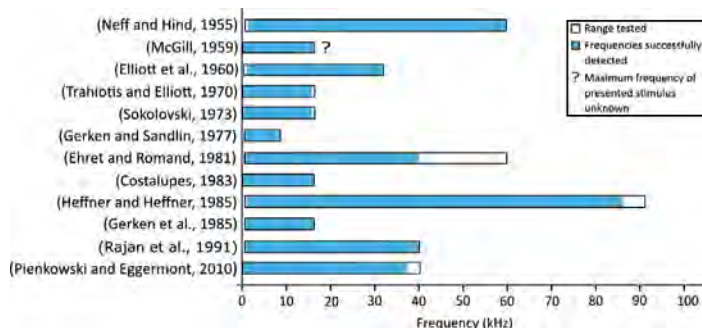
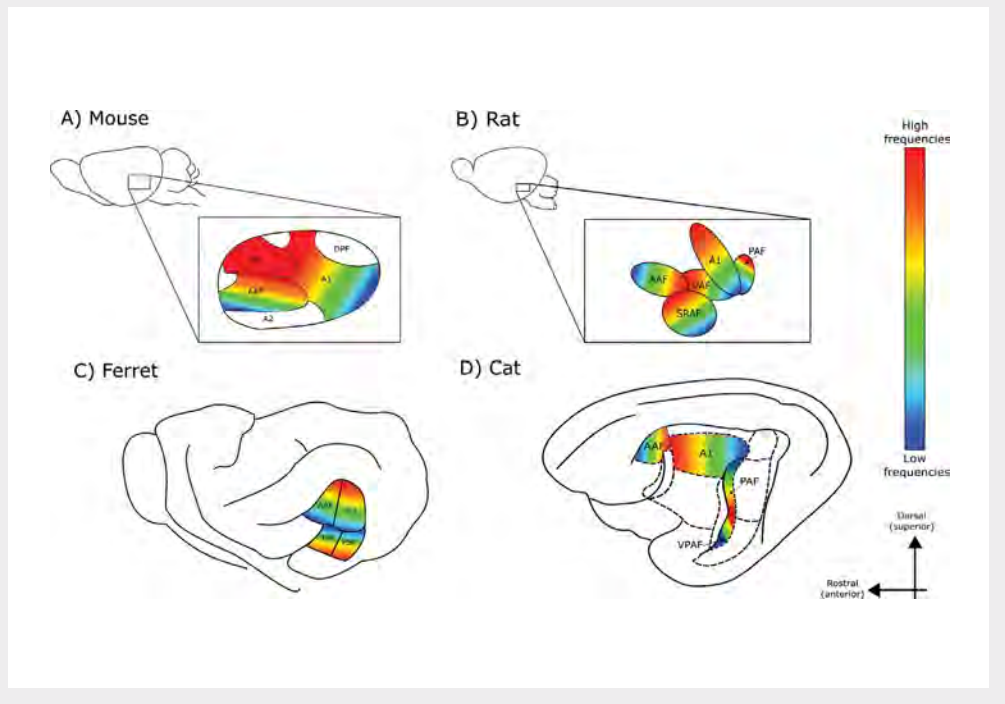


Figure 3. Various reported hearing ranges for cats compared with the range of frequencies of the presented stimuli in each respective study, all of which are cited in References.

Figure 4. The tonotopic organization of the auditory cortex of four mammals. **A:** mouse; **B:** rat; **C:** ferret; **D:** cat. The brains are shown in the sagittal plane and show the primary auditory field (A1), secondary auditory field (A2), anterior auditory field (AAF), dorsoposterior field (DPF), ultrasonic field (UF), posterior auditory field (PAF), ventral auditory field (VAF), suprarhinal auditory field (SRAF), posterior pseudosylvian field (PPF), posterior suprasylvian field (PSF), and ventroposterior auditory field (VPAF).



that the upper hearing limit of cats exceeds 60 kHz and that there could be neurons present in the cortex specialized for these ultrasonic frequencies.

Cortical Representation of Ultrasonic Frequencies

Mice, rats, ferrets, and cats are commonly used as animal models for acoustic research. The biological importance of ultrasound to these mammals is further reflected by the allotment of cortical space for ultrasonic sound perception in their respective auditory cortices. As such, it is crucial to validate as well as expand our current understanding of their hearing abilities, especially the neural correlates underlying the perception of ultrasonic frequencies.

Mice

In the mouse brain (**Figure 4A**), five auditory cortical fields can be delineated in both hemispheres: primary auditory field (A1), anterior auditory field (AAF), secondary auditory field (A2), dorsoposterior field (DPF), and ultrasonic field (UF) (Stiebler et al., 1997). The A1 and AAF regions are both tonotopically organized but with reverse gradients. The properties of the neurons within these two fields are similar. For example, the frequency ranges for neurons found in both the A1 and AAF are between 2 and 45 kHz.

The mouse was the first animal where a specialized cortical region for processing ultrasonic frequencies was identified (Hofstetter and Ehret, 1992). Frequencies between 40 and 70 kHz are represented in the UF, with approximately 50% of neurons responding to frequencies between 50 and 60 kHz. However, unlike the A1 and AAF, the UF is not tonotopically organized (Stiebler et al., 1997), and it is still not clear whether the UF should be considered a part of the primary auditory fields alongside the A1 and AAF.

Tsukano and colleagues (2015) showed that the dorsomedial field (DM), previously thought to be part of dorsal A1, is a separate area specialized for ultrasonic perception. This region contains neurons highly responsive to vocalizations, with frequencies above 40 kHz, demonstrating how certain neurons in mouse cortex respond best to frequencies of behaviorally relevant sound features. This type of cortical organization can also be seen in other rodents that rely on ultrasound for survival.

Rats

The central auditory system of rats is comparable to that of mice in both anatomical and functional organization. Five distinct cortical fields have been identified in the rat brain, and high-frequency neurons can be found in the following regions: A1, AAF, posterior auditory field (PAF), ventral auditory field (VAF), and suprarhinal auditory field (SRAF).

In terms of tonotopic organization, the A1 shows a progression of characteristic frequencies from low (~1 kHz) to high (~60 kHz) along a posterior-to-anterior gradient (Polley et al., 2007). The tonotopic gradient then reverses in a mirror-like fashion at the posterior and anterior borders of the A1 to form the boundaries of the PAF and AAF, respectively (**Figure 4B**) (Rutkowski et al., 2003; Polley et al., 2007).

Unlike mice, an ultrasonic field has not been identified in rats, although, because the tonotopic organization in the rat is comparable to that of the mouse, Kalatsky and colleagues (2005) hypothesized that a distinct region representing ultrasonic frequencies might likely also be present in rats. Overall, despite the similarities between the suggested cortical maps, further investigation is needed to improve our understanding of ultrasonic representations in the auditory cortex of rodents. This could potentially lead to discoveries that could, in turn, be extended to other mammals.

Ferrets

Like the auditory cortex of other mammals, the ferret auditory cortex is divided into multiple subregions. These include the two primary areas, the A1 and AAF (Bajo et al., 2006) and the secondary areas: anterior dorsal field, posterior pseudosylvian field (PPF), and posterior suprasylvian field (PSF). The PPF and the PSF are found immediately ventral to the A1 (**Figure 4C**). Bizley and colleagues (2005) described the functional organization of the different regions within the ferret auditory cortex and subsequently mapped the tonotopic organization of these areas.

As discussed for mice and rats and also for most other mammals, the frequencies in these fields are organized from high to low in a rostrocaudal manner, with frequency reversals taking place at the borders between adjacent fields (Bizley et al., 2005). However, this reversal pattern is not present in ferrets. Instead, the frequencies are organized where the gradients of the A1 and AAF meet dorsally and decrease ventrally (**Figure 4C**) (Kaas, 2011). Therefore, the A1 and AAF are organized tonotopically, with higher frequencies represented toward the dorsal tip. The physiological properties of the ferret A1 (such as tonotopic organization and neuronal properties) are similar to those seen in the cat A1 (Kaas, 2011), but when comparing audiograms of ferrets and cats, the ferret's audiogram is shifted toward lower frequencies (**Figure 2**).

Cats

Similar to ferrets, the cat auditory cortex can be divided into one or more primary areas and several secondary areas (Bizley et al., 2005). To help describe the functional and tonotopic organization of the cat auditory cortex, Reale and Imig (1980) analyzed how clusters of neurons (and sometimes single neurons) respond to various frequencies. In addition to describing the tonotopic organization of the core auditory region, the A1 and AAF, Reale and Imig (1980) also described the presence and tonotopic organization of the PAF and the ventroposterior auditory field (VPAF). Furthermore, they delineated the belt auditory region into the A2, temporal area (T), dorsoposterior area (DP), and ventral area (V).

More recently, Hall and Lomber (2015) confirmed the four functionally distinct tonotopic areas within the cat auditory cortices (A1, AAF, PAF, and VPAF) and reported a reversal in tonotopic gradients between neighboring regions (**Figure 4D**). In the cat, the A1 increases in its tonotopic gradient as it extends from the anterior division of the posterior ectosylvian sulcus (PES) to the posterior portion of the anterior ectosylvian sulcus (AES). At the posterior edge of the PES, the A1 reaches the minimal values of its tonotopic gradient, forming a low-frequency reversal border as it nears the PAF (Hall and Lomber, 2015). High-frequency reversal borders also exist at the A1-AAF and PAF-VPAF borders and are likely a location where ultrasonic selective neurons may be found.

Ultrasonic-Selective Neurons in the Cat Auditory Cortex

Following the principles of tonotopic organization, it seems that neurons with the highest characteristic frequencies could potentially be located at the periphery of each auditory region. Neurons can be classified as being either broadly or narrowly tuned, responding maximally to a large range or a narrow range of frequencies, respectively. This classification provides insight into the type of sensory input the neurons convey and their roles within a specific cortical field. High-frequency selective neurons have been found to be narrowly tuned (Phillips and Irvine, 1982), supporting the claim that high-frequency reversal borders (e.g., between the A1 and AAF) contain mostly such neurons. For example, Carrasco and Lomber (2010) identified neurons selective for frequencies reaching 60 kHz around the border between the A1 and AAF.

However, it is possible that the high-frequency reversal borders also contain broadly tuned subpopulations of neurons, functioning to integrate a wide range of ultrasonic sensory input for both the A1 and AAF. Researchers sometimes avoid probing these regions near the borders to prevent “contamination” from the accidental recording of neurons from neighboring regions (Carrasco et al., 2015). Due to this precaution, studies may fail to record from the neurons with the highest characteristic frequencies, limiting our understanding of the cortical representation of ultrasonic stimuli in cats and other terrestrial mammals.

Conclusion

Ultrasound is essential to the lives of many animals, evidenced by the magnitude of cortical space allocated specifically for ultrasound in some species. Despite the biological importance of ultrasound, researchers might have been underestimating the ultrasonic hearing abilities of many terrestrial mammals. It is therefore also possible that the extent of the ultrasonic abilities of some terrestrial mammals, as discussed in this article, has not yet been conclusively established. Until this matter is clarified, the location in the brain where these frequencies are encoded also remains uncertain. Further investigations may elucidate uncertainties in our understanding of the role of ultrasonic frequencies in auditory neuroscience as a whole.

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About the Authors



M. Charlotte Kruger

charlotte.kruger@mail.mcgill.ca

Department of Physiology
McGill University
Montréal, Québec H3G 1Y6, Canada

M. Charlotte Kruger graduated from the University of Western Ontario (London, ON, Canada) with a BSc Honors Specialization in Biology in 2019. She is a current graduate student in the Cerebral Systems Laboratory at McGill University (Montréal, QC, Canada). She is investigating the ultrasonic hearing abilities of the cat and the location where ultrasonic frequencies might be encoded in the cat brain, to better understand the role of ultrasonic hearing in auditory neuroscience.



Carina J. Sabourin
carina.sabourin@mail.mcgill.ca

*Department of Physiology
McGill University
Montréal, Québec H3G 1Y6, Canada*

Carina J. Sabourin graduated from Queen's University (Kingston, ON, Canada) with BSc Honors Specialization in Life Sciences. She recently joined the Cerebral Systems Laboratory at McGill University (Montreal, QC, Canada) as a graduate student pursuing an M.Eng in Biological and Biomedical Engineering. She is using awake electrophysiological recording techniques to investigate the auditory cortex in animal models. She is currently using system identification methods to model the temporal modulation of auditory neurons in response to biologically important sounds.



Alexandra T. Levine
alevin23@uwo.ca

*Department of Psychology
Western University
London, Ontario N6A 3K7, Canada*

Alexandra T. Levine is a postdoctoral associate in the Neuroplasticity in Sensory Systems Lab (NiSSL) at Western University (London, ON, Canada) researching brain plasticity following sensory loss. She is currently working on a range of projects involving

ultrahigh-field magnetic resonance imaging (MRI), including structural and functional differences in the brain resulting from hearing loss and neural correlates of behavioral advantages seen in such individuals. She received her BSc in psychology and cognitive neuroscience from The University of Nottingham (University Park, Nottingham, UK) and her MSc in cognitive neuroscience and PhD in cognitive neuroscience and neuroimaging from the University of York (UK).



Stephen G. Lomber
steve.lomber@mcgill.ca

*Department of Physiology
McGill University
Montréal, Québec H3G 1Y6, Canada*

Stephen G. Lomber is a professor of physiology at McGill University (Montréal, QC, Canada) where he holds the Canada Research Chair in Brain Plasticity and Development. Dr. Lomber received his BSc from the University of Rochester (NY) and his PhD from the Boston University School of Medicine (MA), both in neuroscience. Dr. Lomber's laboratory (www.cerebralsystems.ca) uses an integrated approach of psychophysics, electrophysiological recording, neuroanatomical approaches, and functional imaging to examine multisensory processing in auditory cortex. Work in the laboratory examines cortical plasticity in the presence and absence of acoustic input and following the initiation of auditory processing through the use of cochlear prosthetics.

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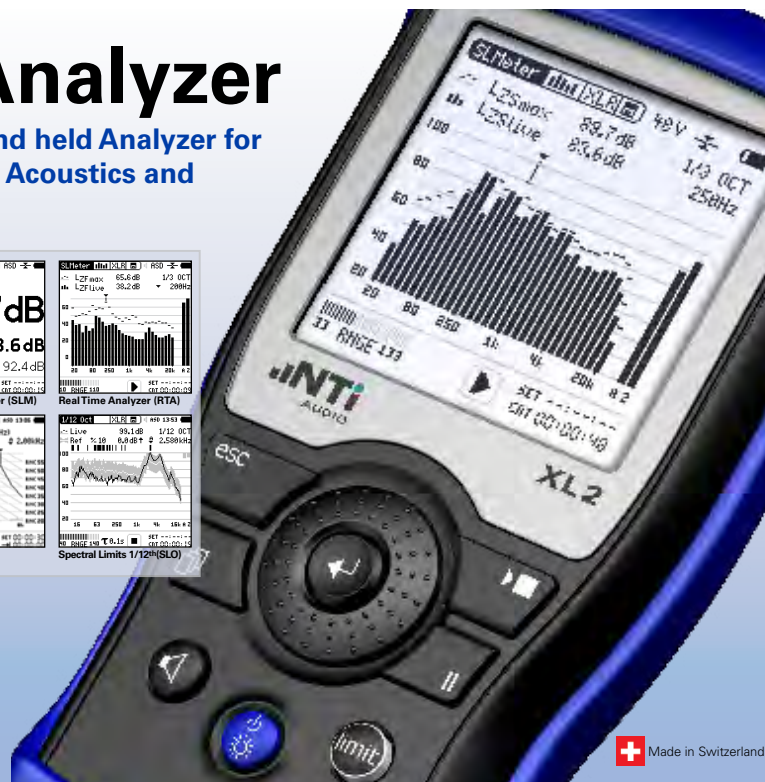
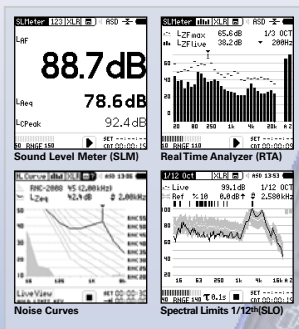
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Japan
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