Physiological Acoustics

How nature makes sense of sound

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The sense of hearing plays an important role in our everyday life. Hearing impairment is a big and ever-growing global problem – with severe personal and socio-economic consequences. Various technologies have been developed to improve hearing for listeners suffering from a hearing loss. But their performance still falls short relative to healthy hearing, especially in the presence of multiple sound sources. How comes? Decades of research continuously improved our understanding of the sense of hearing. But more and more model-based approaches fail to provide the predicted benefit. Physiological acoustics approaches this challenge with a focus on physiological boundary conditions. The goal is to identify the mechanism utilized by nature to solve this problem. The physiology of the hearing system is outlined and the inclusion of the ubiquitous physical phenomenon of entrainment into models of hearing is discussed. This, from currently established models, deviating approach might remove some of the limitations of current models and might open up for a broad variety of applications in health science and audio technology.

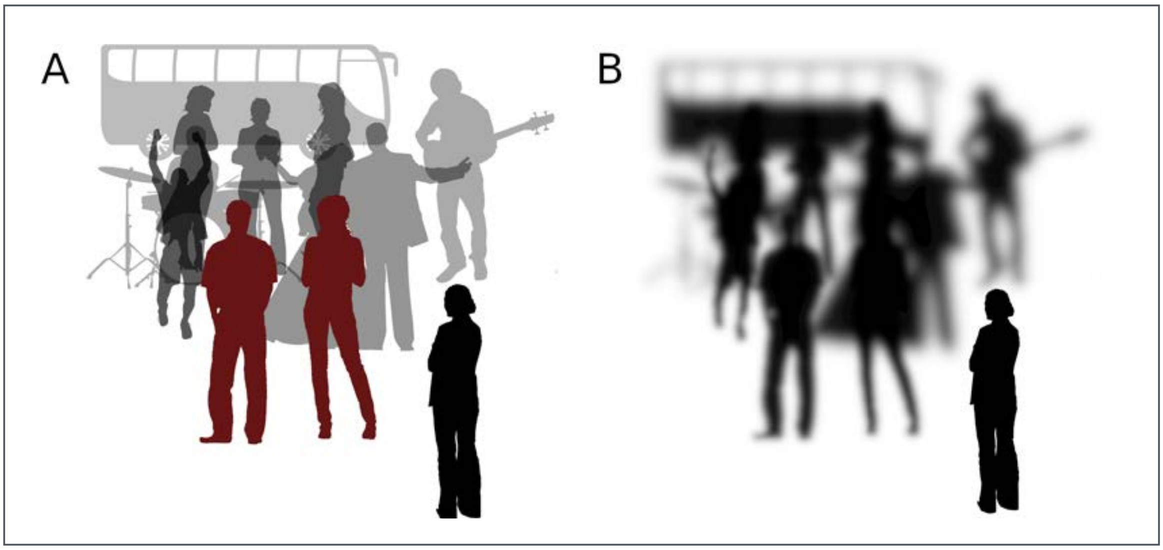
The facets of hearing

Physiological acoustics and relevance of hearing research

The sense of hearing is key to communicate by means of sound. Pressure variations in air and matter inform about the presence of predators, sources of food, and transmit the beauty of a voice and music. Nature developed unique sensor- and information processing devices built on the principles of physics and maximizing performance within the limitations of biology. The relevance of hearing becomes salient when hearing is impaired or lost. Normal hearing listeners can easily separate a moving car and music from the voice of the person they are talking to. Hearing impaired listeners lose this ability to a certain extent and perceive a more “blurred” acoustic image of the environment (figure 1). This challenge is often referred to as the “cocktail party problem” – more focused on the communication than the cocktails.

Hearing loss has also implications that lead to social isolation and cognitive decline [1]. Hence, it is not only an individual challenge, but a challenge for our global society in a world with increasing noise exposure caused by ships, cars, buildings, and lifestyle. The World Health Organization (WHO) projects that 2.5 billion people will have some degree of hearing loss, and that 10 % of the human population will have a disabling hearing loss that will exclude them

Fig. 1: A visual analogue of a complex acoustic scene with a number of simultaneously active sound sources.
A) A normal hearing listener can separate the sound sources into a relevant sound to attend to (red) and a background (grey).
B) A listener with hearing impairment cannot separate sound sources and will perceive a “blurry” sound image where it is impossible to attend to a single source.

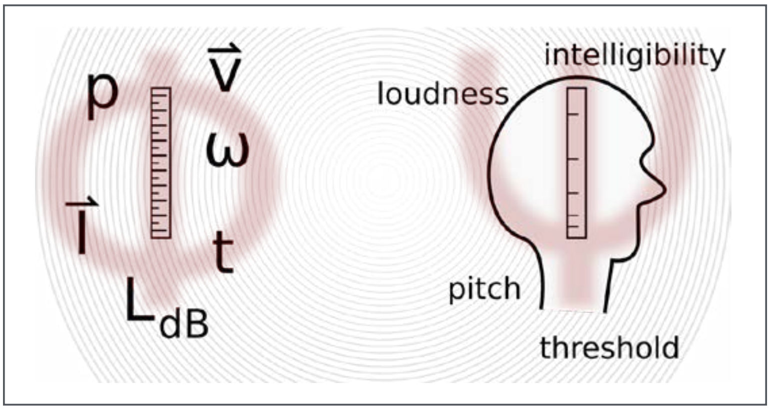


from social interaction [2]. This is still a relevant problem to solve!

A lot of progress has been made in the field of hearing during the last decades – and the field has spread out and incorporated even more disciplines. Descriptions of the processing of sound by using engineering techniques have led to numerous models of hearing. They provide a basis for the development of hearing assistive technology like hearing aids and cochlear implants. However, these devices cannot enable listeners to perceive the same "sharp" acoustic image of the environment, and too many people still suffer from hearing impairment, despite technological development.

The field of "physiological acoustics" can be regarded at as the approach to solve the "cocktail party problem" by mapping principles from physics onto the function and natural limitations of biology. It benefits from other approaches applying various levels of detail. These include, among others, psychoacoustics that maps sound directly to perception in a "black box approach", physiology that investigates the biological function of the organism, and from the mathematical description of sound used in acoustic signal processing. The goal of physiological acoustics is to map, describe and mimic how nature processes sound in the biological system of hearing. This will help to identify the key mechanisms and key phenomena that can be used to implement solutions and to restore hearing as much as possible using audio-, neural-, and biotechnology. Building solutions on the same principles used by nature will have implications not only for the health sector, but also improve everyday communication, improve virtual reality and significantly reduce the resources required to process sound. In short – a modern discipline within acoustics!

Fig. 2: Psychoacoustics projects the physical metrics used to describe a sound field (pressure, intensity, frequency, …) onto perceptual quantities (loudness, pitch, …). Perceptual measures are usually influenced by various physical parameters. Hence, perception can be considered to be a projection of one multidimensional (physical) space into another (psychometrical) space. Fundamental in psychoacoustics is that the "system as a whole" is evaluated.



Psychoacoustics and acoustic signal processing – here be dragons

A corner stone in hearing research is psychoacoustics, e. g. [3]. Psychoacoustics can be considered a chimera of psychology and physics – or psychometrics and metrology. It investigates the effect of a sound (a stimulus) on perception (figure 2). This is particularly important because it evaluates the "system as a whole" by correlating a physical measure with a behavioural measure.

One prominent example is sound pressure level. Sound pressure level is related to the physical energy in the stimulus. In hearing, the information in the stimulus is processed by the whole hearing system and finally evaluated by the listener by answering the question "How loud is that signal"? Sound pressure level is, however, not the only relevant parameter for loudness. Loudness changes as a function of frequency, bandwidth, temporal properties, and even context. Hence, multiple physical dimensions need to be mapped onto perceptual dimensions – and this requires careful experimental design and control of the physical parameters of the stimulus. And even though various prediction models of loudness exist [4, 5], it is, especially in realistic environments, still not possible to reliably predict the perception of loudness (see, e. g. [6] for a review). A relevant task for everything from office rooms to the noise generated by sustainable energy sources.

Here, acoustic signal processing plays an important role. It is a mathematical method to describe, analyse, and manipulate sound signals. The precise manipulation of a specific stimulus property allows to investigate the correlation of this sound property with perception.

There are numerous suggestions for where and how certain psychoacoustically measured effects are processed in the physiological system. Ultimately, all these ideas are based on some postulated function or a correlation between the activity of single neurons, or groups of neurons, and the behavioural measure. The first challenging aspect of this approach is that psychoacoustics always evaluates the system as a whole – while physiological studies focus on individual elements of the highly interconnected system. Hence, given the high number of neurons in the auditory system, one cannot be sure that the response of a single neuron in a complex system is relevant. The second point to consider is that acoustic signal processing is completely free of any biological boundary conditions. While mathematical elegance can be attractive to describe hearing, it is challenging to correlate it with physiology. So far, no evidence for complex numbers in the brain was found – but it is a useful concept to describe sound signals.

Despite all these pitfalls serves psychoacoustics as the ultimate test of any technological development within hearing science. A hearing impairment compensation technique is only successful if it restores the desired aspects of perception. And even solutions that are far from physiologically plausible, like recent developments within deep neural networks, will serve a purpose. But it is important to remember that this will not necessarily identify the way by which the hearing system is implemented by nature.

Human auditory anatomy and physiology in a nutshell – the snail in your head

To better appreciate the complexity of the hearing system, a view into physiology is instructive. The physiology of the human hearing system, commonly referred to as human auditory physiology, is rather unique in that it spans a broad variety of domains. From a structural point of view, it contains visible elements like the pinna and the ear canal (figure 3).

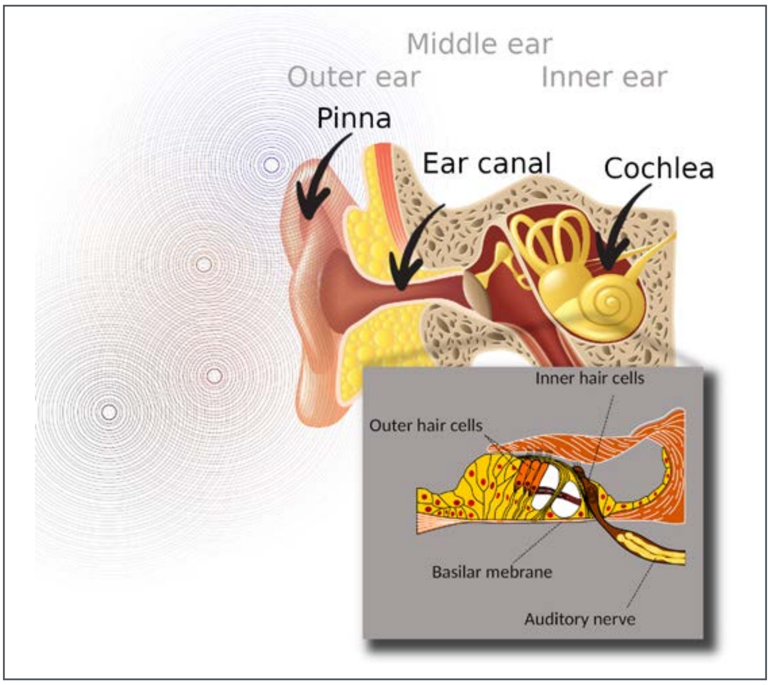


Fig. 3: Anatomy of the outer-, middle-, and inner ear. A mixture of sound waves enters the ear canal and is spectrally formed by the pinna. The vibrations in air excite the middle ear which excites an oscillation in the inner ear, the cochlea. Along the length of the cochlea, the organ of Corti is located with an arrangement of three rows of outer hair cells (OHC) and one row of inner hair cells (IHC). Action potentials generated through mechano-electric transduction are passed on through the auditory nerve to the brain. (Organ of Corti modified from https://commons.wikimedia.org/w/index.php?curid=6888273 by "Madhero88 – Own work", CC BY-SA 3.0,)

The small bones in the middle ear link air-borne sound to structure-borne sound. From there, the sound energy is transferred into the fluid-filled structure in the inner ear containing the snail-shaped structure of the cochlea. Within the cochlea, specialized cells translate the mechanical vibration into a neural signal. From here on and towards the brain, the signals are passed on to a wide network of groups of interconnected neurons (nuclei). These nuclei are not only connected towards the direction of the auditory cortex, but also communicate "backwards" to earlier stages of processing, all the way down to the inner and middle ear where they affect the activity of hair cells and the mechanical impedance of the middle ear. Physiological acoustics targets all these parts of the auditory system. In the following, we will focus on sound processing of the mechanical parts of the system and its special role as a bottleneck of information.

Sound processing already starts at the pinna where the incoming wave is reflected at the complex surface before funneling the sound wave into the ear canal. In the spectral domain, this can be observed as a shaping of the spectrum which depends on the angle of incident. Hence, this filtering process already provides information about the location of the sound source before even entering the ear canal. This information is individually different – this means that it is hard to "hear with the ears" of others. But with some training, the auditory system can even adjust to such a modification [7].

The middle ear connects the ear canal through the tympanic membrane to the inner ear through the oval window. The arrangement of the bones and the size of the membrane surfaces allows to maximize the energy transfer between the two media, liquid and air with heavily differing densities and therefore impedance. High efficiency in the energy transfer from air to fluid is desirable to maximize the sensitivity to detect sounds. Humans can detect everything from a small needle falling to the ground (approximately 20 µPa of pressure amplitude) up to the sound of a jumbo jet at take-off (over 20 Pa of pressure amplitude). For high sound intensities it might be detrimental to transfer too much energy into the middle ear. A too high energy influx can damage inner ear structures. To avoid this, the hearing system can actively change the properties of the middle ear in the case of too high energy influx by contracting a small muscle. This stiffens the mechanical chain in the middle ear, reduces transmission and increases reflection.

The inner ear consists of a system of three fluid-filled chambers. One chamber is separated from the other two by a membrane which changes in width and mechanical properties along the length. In a simplified view, this fluid-embedded membrane has a gradually changing impedance and hence displays a frequency-dependent response to the incoming sound. This means, that when the stimulus is a pure tone, the maximum vibration will change when changing the frequency of the tone. In a first approximation, the inner ear can hence be viewed at as a mechanical frequency analyzer. The vibration of the basilar membrane is often referred to as the "macromechanics" of the inner ear. The gradual change in the mechanical properties of the inner ear is implemented such that the transmission is maximally efficient [8] and that the overall pattern evoked by a tone in the inner ear looks approximately the same, but is only translated along the length of the inner ear [9]. Nature solved a complex optimization problem.

The key to performance and the genius of the inner ear lies in the "micromechanics". A closer look at one location of the basilar membrane (figure 3) reveals a unique arrangement of specialized cells. This arrangement is called the "organ of Corti". In simplified terms, the organ of Corti is displaced by the vibration of the basilar membrane. Functionally, it transforms this vibration into a complex mechanical interaction, finally leading to the generation of electrical signals, so-called action potentials, by the inner hair cells (IHC). These action potentials with the relevant information about the sound are then passed on to the attached auditory nerve. There are some key elements in that process. A main contributor lies in the group of outer hair cells. These unique cells have the ability to change their length and hence act as active devices – this means that they are moving while you hear a sound. Contraction and elongation of the cell body optimizes the generation of action potentials and thereby improves not only the sensitivity, but also the selectivity of the hearing system. Hence, the inner ear is an active sensor with outer hair cells actively pushing and pulling on the basilar membrane – with the correct timing to optimize processing by the inner hair cells. Another element is that the chambers separated by the basilar membrane show a voltage gradient. This "physiological battery" provides the energy source for the mobility of the outer hair cells (OHC). A very efficient, but also fragile construction.

Yet another property that makes the inner ear both attractive and complex is the fact that its processing properties change with input level. This means that the system is highly nonlinear! At high input levels, the response is highly dominated by the passive mechanical parameters. At low input levels, the system is able to provide an effective gain of up to 50 dB! At these low input levels, the excitation on the basilar membrane is very narrow while it broadens towards higher input levels. In case when damaged, the inner ear loses the ability to amplify and acts purely linear. This is a good example of an efficient and elegant solution where low intensity sounds are heavily amplified, while sounds with high intensity are processed passively – or even attenuated with the help of the middle ear.

The inner ear – how special is it?

The way in – the function of mechano-electric transduction

The most relevant task of the inner ear is to transmit information towards the brain. From a mathematical point of view, a sound signal is a one-dimensional source of information. The task of the inner ear is therefore to transduce, preprocess and preserve all the relevant information in that signal. This is implemented by a combination of the mechanical place-frequency mapping, active amplification and distribution of the mechano-electrical transducers along the whole length of the inner ear. Mechano-electrical transduction is done by inner hair cells of which there exist around 3 000 in the human inner ear. Each hair cell is connected to around 10 nerve fibers that transmit the generated electrical action potentials to the brain. This means that the one-dimensional sound signal is transformed into a set of about 30 000 channels of neural information! The task of the interconnected nuclei following the inner ear is then to further process this information, finally leading to the perception of sound we know.

Computational models help to conceptualize this complex process. Such numerical models are successful in accounting for a variety of measurable phenomena and found application in numerous technological applications like, for example, the development of the "MPEG2 – audio layer III" codec (MP3). Depending on their focus, different assumptions need to be made. The key focus of most models is place-frequency mapping. The concept is as elegant as it is simple: Consider one place on the inner ear. Determined by the mechanical properties, this place will show maximum amplitude for a specific frequency when a pure tone is played. The amplitude will be lower when the frequency of the tone is either increased or lowered. Based on this, one can define a "frequency response" of this place and formulate this in mathematical terms as a "transfer function" in the frequency domain. Doing this for a variety of places leads to a collection of filters – a filter bank. Each of the filters can be considered an independent "channel" which can be further processed and manipulated.

Problem solved? Not quite. These models are successful, but they imply a large number of assumptions – many of which are mathematically convenient, but physiologically implausible or questionable in the light of more recent data. One critical assumption is that the response to a complex sound can be derived from the mapping established by presentation of pure tones. This means that one assumes that a sound that consists of multiple tones will evoke an oscillation in the inner ear that looks like the superposition of the oscillations of each of the tones in isolation. These (linear) models exclude phenomena where the oscillation evoked by one tone can be influenced by the oscillation by another tone, often referred to as "suppression". More elaborate models exist that account for some of these aspects of the nonlinearity of the inner ear. They compensate for some of the shortcomings of linear models on cost of increased number of parameters. The second critical assumption is that humans' ears are very similar to chinchillas and guinea pigs. Most data exist from animal models like guinea pigs and mice – while hardly any observations of human inner ear mechanics have been made since the efforts of Georg van Békesy in the late 1960's. Maybe with the current approaches, we are effectively trying to restore hearing of a beast that is a mixture of guinea pig, mouse, cat, and human.

The way out – otoacoustic emissions

Usually, the ear is considered a "microphone" in the sense that it receives a sound signal and transforms it into an electrical signal. The ear of many mammals and non-mammalian species (even insects!) do not only receive sound, but also emit sound! Placing a microphone into the ear canal of a human listener will, with a probability of over 70 %, allows recording a sound signal that reminds of the sound of a vacuum cleaner, e. g. [10]. These sound signals are generated in the inner ear and are often referred to as "spontaneous otoacoustic emissions (SOAE)". The amplitude spectrum of SOAEs reveals narrow distributions of energy across a broad frequency range. Why are they there? And where do they come from? Taking into consideration that the inner ear is active and highly tuned might provide a hint. The presence of an SOAE in the ear canal dictates, based on reciprocity, that there needs to be an oscillation in the inner ear – which energy travels through the middle ear into the ear canal where it can be recorded. And the elements of nonlinearity and an active source (which are required for the high sensitivity) make it plausible that such a system can enter a self-sustained oscillation – either by noise excitation or by entering an intrinsic limit-cycle oscillation as often observed in complex dynamical systems.

Otoacoustic emissions (OAEs) are considered an artifact and non-informative regarding the function of hearing. But even though often considered an artifact, OAEs provide a window into the function of the inner ear. They can serve as a "remote sensing" method where sound is sent into the system and the reflected sound is analyzed to derive properties of the system. This is analogue to electromagnetic devices like radar or lidar. OAEs are today used in standard newborn screening, audiological diagnostics and even considered for technological application to act as the "acoustic fingerprint" of an individual.

Current models of hearing struggle to account for the increasing body of data reaching the field of hearing from various directions – and most of them neglect the presence of OAEs. The intrinsic and often implicit assumptions and simplifications made by the models can be a reason for the relative stagnation in the ability to restore hearing for hearing-impaired listeners. Perhaps, the field of physiological acoustics can contribute to the process of evaluating the assumptions and implications of the last decades of hearing research considering the increasing body of physiological insights.

The balance between elegance and complexity

Appreciating the sense and the physiology of hearing in all its complexity highlights the necessity to continuously consider which conclusions can be drawn. The evidence derived from a given experiment can never be stronger than the method applied. Obviously, assumptions need to be made based on the currently available data. When interested in the physiology of hearing, the field of physiological acoustics needs to balance between the elegance and the complexity of a method. An elegant method can allow for precise predictions of individual parts of the system. Describing the place-frequency mapping in the cochlea with a transfer function is elegant because it allows for efficient processing of arbitrary signals efficiently. On the other hand, a complex method might be a more precise description of the system including various phenomena. Describing the cochlea as a 3-dimensional system with air-fluid-structure coupling might be precise within the boundaries of known parameters but is hard to handle and interpret.

Physiological acoustics contribute to test many of the important conclusions drawn from the last decades of hearing research. Recent approaches were successful to link physiological and psychoacoustical data using models that allow to account for OAE data, provide reasonable control of the mechanics in the inner ear, provide plausible neural response patterns, and even allow to predict non-invasive electrophysiological responses in human listeners [11, 12]. While still simplified and based on assumptions such an approach can provide direct testable predictions across fields and species. The price to pay is computational complexity and the requirement to estimate unknown physiological parameters.

Going one step further – are there "first principles of hearing"?

There is broad consensus that a key element in healthy hearing is the ability to amplify weak sounds. Overexposure to noise, ototoxic drugs or genetic defects affecting the integrity of the OHC motility leads to a reduction in amplification and hence a hearing impairment. One of the still most relevant questions is: *Which physical principles are used by the auditory system?*

And, in the light of an evolutionary argument assuming optimization and natural selection:

Are there any "basic" principles that are used in all physiological information processing systems?

A promising path can be found in the field of nonlinear dynamical systems. Efforts to model the behaviour of bullfrog hair cell motility lead insightful experiments that link knowledge from physics to the key element in physiological sound processing. A basic element in this approach is to describe a system (the hair cell in this case) in a way to allow for various patterns of behaviour. Depending on the imposed parameters, such nonlinear dynamical systems can behave like a damped oscillator (like a mass-spring-damper system or a linear filter), oscillate in a non-harmonic way (like a mass-spring-damper system with amplitude-dependent parameters or a non-linear filter), or even oscillate spontaneously [13].

What justifies the increase in complexity relative to linear formulations using transfer functions? Both descriptions can account for certain aspects of tuning, compression and frequency selectivity. But only a description based on nonlinear dynamical systems provides an integrated view on experimental data where there is a strong link between OAEs and psychoacoustics – and potentially neuroscience. A prominent example is an early finding that the mean frequencies of SOAE peaks coincide with the most sensitive frequencies of the same listener [14]. A filter bank approach can account for such a frequency-dependent sensitivity but cannot account for SOAE. An approach based on nonlinear dynamic systems can provide an explicit link between these two phenomena [11].

Systems of coupled nonlinear and active oscillators also display another phenomenon that might allow reinterpreting both physiological and psychoacoustical data. In a nutshell a spontaneously oscillating system can be "forced" to change its intrinsic frequency when coupled to other oscillators (see figure 4). This effect of "entrainment" [15] and "clustering" has been observed broadly in various fields, including in a system of coupled clocks and in neuroscience in connection to diabetes [16], to name a few. It has also explicitly been applied to model the hearing organ of amphibians and properties of SOAEs in these species [17].

One might speculate that such phenomena might be advantageous for the sense of hearing. High sensitivity can be achieved by amplification and adaptive tuning. Relevant frequencies can be "improved" by entraining parts of the inner ear towards dominant frequencies. This could potentially improve neural coding and hence the interpretability of the neural signal by the brain. A filter-based approach is based on the phenomenon that one sound can be made inaudible by another sound by the choice of an (arbitrarily chosen) signal-to-noise ratio. In a system of coupled oscillators can this phenomenon explained purely by the entrainment of oscillators. Such a (so far speculative) mechanism might save resources to process irrelevant information and hence be one of the reasons underlying the efficiency and precision of the sense of hearing.

New insights from physiology, physics, mathematics and novel measurement techniques might provide the required insights to re-interpret the sense of hearing in a way where observable phenomena can, in parts, be derived from a limited set of physical principles that are universal to nature. This will allow to mimic the principles of nature in technological applications. It can also help to restore a necessary mechanism in information processing (rather than an isolated observable phenomenon), and hence get us closer to solving the challenge of hearing impairment.

Current challenges and opportunities

The field of hearing research and, in particular, physiological acoustics can provide the basis for some groundbreaking developments for a benefit of society. In the following, few highlights will be presented that might outline important directions for the upcoming years.

In the health sector

Physiological acoustics provides a direct link to how nature implements sound processing in physiology. Access to these mechanisms will allow to design and implement increasingly sensitive diagnostic methods. Damages and deficits can be detected earlier and met with a suitable compensation or therapy.

Current challenges that need to be solved are, for example, that the largest amount of knowledge stems from other species than humans. Even though similar to human anatomy, the evolutionary relevant challenges are different between guinea pigs, cats, and humans. Another factor might be the use of anesthesia in neuroscience. The drugs applied during the experiments might change the neural activity and hence mislead our interpretation of the data. In general, little details are known about human auditory physiology – mainly due to obvious ethical reasons. Neither the mechanical nor the neural code of human hearing is cracked! This might have direct consequences in clinical audiological practice.

Physiological acoustics can help to improve non-in-

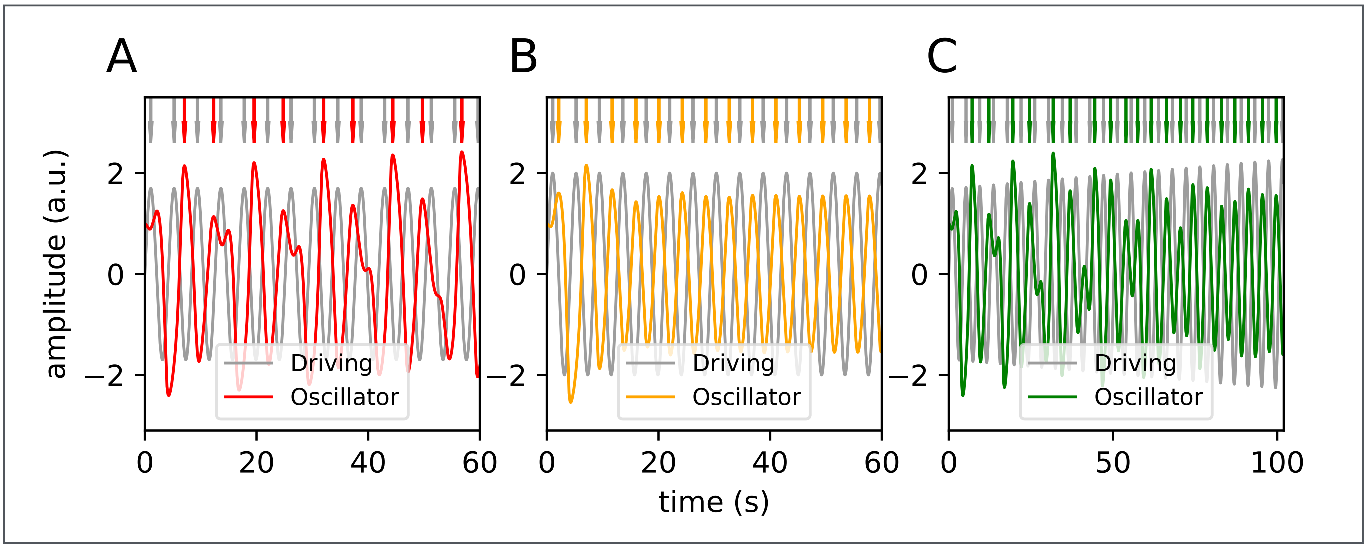


Fig. 4: Interaction of a self-sustained oscillator (coloured) with a harmonic driving force. The oscillator (coloured) is driven by the external driving force (grey). The arrows on top indicate the periodic maximum. In this example, a van der Pol oscillator was used. The scale is arbitrarily chosen and can be freely scaled by the oscillator parameters.
A) The driving leads to a superposition of the oscillator frequency and the driving force frequency, resulting in a "beating" effect. The oscillator keeps its intrinsic frequency.
B) With an increased driving force amplitude, the oscillator is forced into entrainment with the driving force and the oscillator adopts the driving force frequency.
C) Transition from "beating" state (low driving amplitude) to "entrained" state at higher amplitudes. Simulations made by Lene Højberg Christensen and Jonas Birkedal Dudal Jensen.

vasive measurement techniques based on otoacoustic emissions and electrophysiology. When the relevant processes underlying hearing can be understood, sensitive metrics can be defined that are closer to the mechanisms used by nature than the metrics used by engineers! And with proper therapeutic tools it will be possible to restore the ability of the relevant parts required to utilize the basic mechanisms underlying hearing. It might be better to restore hair cell motility and all consequences thereof (like entrainment) rather than only the aspect of amplification or selectivity in isolation.

In technology

From an audio-technological perspective, it is desirable to capture the relevant aspects of sound while limiting computational effort. Hence, it might be beneficial to include certain processing on the level of the sensor rather than recording a sound signal and then processing the information by a computer afterwards. First approaches exist that try to mimic inner ear processing within micro-mechanical system design, e.g. [18]. A mechanical beam with feedback behaves in parts like a hair cell and can show high tuning and sensitivity. A system of such sensors might behave similar to the inner ear and hence provide an optimized, pre-processed stream of information about the sound signal picked up by the sensor. Such a sensor would save a tremendous amount of energy in wearable applications like hearing aids and cochlear implants - and might even improve encoding of audio information for transmission. The latter can directly contribute towards improved communication in challenging environments. One might also consider that such technological devices directly mimic the function of the inner ear and hence replace a defective physiological element.

Summary and conclusions

The sense of hearing is highly relevant for everyday communication and it is also threatened by increasing sound exposure and environmental factors. The physiological implementation of sound processing (the "auditory system") displays high efficiency and precision while complying with strict biological limitations. Physiological acoustics is the interdisciplinary approach to reveal the biophysical principles underlying hearing – with the goal to restore and mimic the basic underlying principles that allow communication in complex acoustical environments. Principles from physics can be transferred to hearing and can overcome limitations of current approaches to describe and model hearing. Hence, hearing research and physiological acoustics can be considered one of the modern and relevant hubs for health and innovation for the benefit of society.

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