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Responses of the Inner Ear to Infrasound

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Abstract

Unweighted sound measurements show that wind turbines generate high levels of infrasound. It has been wrongly assumed that if subjects cannot hear the infrasound component of the noise then they cannot be affected by it. On the contrary, the mammalian ear is highly sensitive to infrasound stimulation at levels below those that are heard. Most aspects of responses to infrasound are far from well established. Measurements made within the endolymphatic system of the cochlea show responses that become larger, relative to measurements made in perilymph, as frequency is lowered. This suggests that endolymphatic responses to infrasound are enhanced in some manner. For high-frequency sounds, acoustic stimuli in the ear are summed. In contrast, the inner ear's responses to infrasound are suppressed by the presence of higher frequency stimuli. The complexity of the ear's response to infrasound leads us to the conclusion that there are many aspects that need to be better understood before the influence of wind turbine noise on the ear can be dismissed as insignificant.

Introduction

The effects of sounds on humans are typically evaluated through measurements made with instrumentation such as microphones and sound level meters. As the vast majority of these measurements relate to sounds that people can hear or which may damage the ear, measurements are routinely weighted according to the hearing sensitivity of humans (i.e. the A-weighting curve which is based on the 40 phon audibility curve in humans). As the ear represents the highly sensitive sound detector of the body, it has been widely assumed that if a sound is not detected (i.e. the sound is not heard by a listening subject) then the sound has no relevance to human physiology. This concept was further developed with respect to whether harm could arise from sounds and has been widely expressed in the form of statements along the lines of "what you can't hear, can't hurt you". The origins of this belief are

difficult to trace but it is believed to originate from the title of a newspaper article by an engineer making measurements of the “Kokomo hum” in 2001 (Alves-Pereiraa M, Castelo Branco, 2007). It is important to realize that the concept was not based on physiologic scientific studies in which “harm” was quantified or measured in some way that correlated with low-frequency sound measurements. Rather, the statement was a speculation without any fundamental consideration of how the ear works. Indeed, it is quite remarkable how such an erroneous concept could have gained such widespread acceptance when there is such a large amount of physiological data showing that the ear’s response to low-frequency sounds is far more complex than that of a simple microphone (reviewed by Salt and Hullar, 2010).

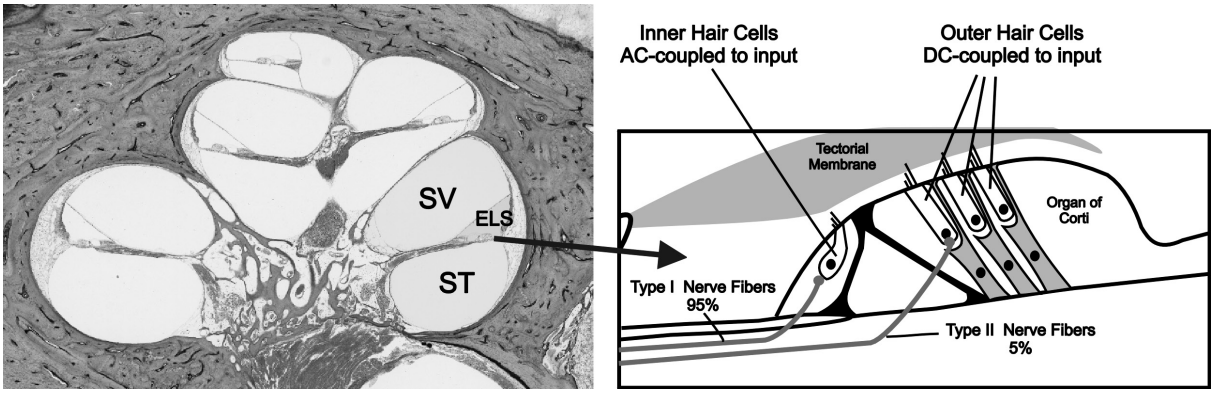

Figure 1: Anatomy of the Inner Ear. ***Left:*** *A mid-modiolar section of the human cochlea spiral with the compartments of one turn labelled. SV:scala vestibuli; ELS: endolymphatic space; ST: scala tympani. The structure containing the sensory cells, called the organ of Corti, is on the lower border of the ELS.* ***Right:*** *Enlarged schematic of the organ of Corti, which contains two types of sensory cells. The sensory hairs of the outer hair cells are embedded in the gelatinous tectorial membrane making them DC-coupled to the input stimulus. The hairs of the inner hair cells are free within the fluid space below the membrane, causing them to be AC-coupled to the input stimulus. Histological image courtesy of Saumil Merchant, MD, Otopathology Laboratory, Massachusetts Eye and Ear Infirmary and Harvard Medical School, Boston.*

The anatomic features of the inner ear that are relevant to its sensitivity to low-frequency stimulation are summarized in Figure 1. The important feature is that the sounds that are heard are mediated through the inner hair cells and transmitted to the brain through the Type I nerve fibers which make up the majority (95%) of the auditory nerve. In simple terms, the inner hair cells are AC-coupled to the mechanical stimulus, meaning that they respond well to high stimulus frequencies but are insensitive to very low-frequency or sustained displacements of the organ. Based on single nerve fiber recordings, Temchin et al., 1997 concluded that a high-pass filter was interposed before the site where auditory nerve excitation thresholds were determined. A consequence of this arrangement is that subjective hearing is insensitive to stimuli of infrasonic frequencies because of the high-pass filter/ AC coupling. However, because the outer hair cells of the ear are DC-coupled to the stimulus (sensitive to high-frequency stimulation, low-frequency stimulation and sustained displacements of the organ), their characteristics can indeed render the ear sensitive to infrasound. It has been shown that prolonged displacements of the

organ of Corti for 20 minutes or longer, by microinjection of gel into the cochlear apex, cause endocochlear potential changes that were sustained throughout the procedure (Salt et al, 2008). This confirms the ability of the outer hair cells to respond to slowly occurring or sustained displacements. The outer hair cells are mechanically coupled to the inner hair cells and are innervated by so called Type II fibers that make up 5% of the auditory nerve.

The fact that hearing is insensitive to infrasonic frequencies therefore does not indicate that the entire ear is insensitive to infrasound. This is analogous to viewing the electrical output of a low-frequency-capable sound level meter on an AC-coupled oscilloscope and concluding that the sound level meter is “insensitive” to low-frequencies. Similarly, because subjective hearing is based on an AC-coupled output from the ear, that does not mean that an unheard infrasound cannot influence the other components of the ear, such as the outer hair cells, and thereby influence heard sounds in a number of complex manners, as discussed below. Here we present a number of different measurements that characterize a number of aspects of the ear’s sensitivity to infrasound.

Methods

The electrical measurements from the inner ear we present in this paper include data from guinea pigs and cats. In guinea pig experiments, stimuli were generated and responses were recorded using Tucker-Davis System 3 hardware controlled by custom-written software on a PC. Sound stimuli were generated in a closed system, using a hollow ear bar between the transducers and the external ear canal. Full technical details of stimulus generation are given elsewhere (Brown et al., 2009). Cochlear responses were measured from electrolyte-filled glass pipettes, inserted into the cochlear fluids spaces, via a high input impedance electrometer.

Single nerve fiber recordings in cats followed methods described by Kiang *et al.* (1965). Low-frequency (i.e., 50 Hz) tones were presented to cat ears with a DT48 headphone coupled to the ear through a hollow ear bar.

Guinea pig experiments were approved by the Animal Studies Committee of Washington University. Cat experiment protocols were approved by the Animal Care Committee of the Massachusetts Eye and Ear Infirmary.

Results

1) Endolymphatic enhancement of responses to low-frequency sounds.

In this study, we measured electrical responses from the basal turn of the guinea pig cochlea in response to tones of varying frequency. Sound levels were varied until a specific response amplitude (500 μV) was generated. These sound level thresholds were measured in scala media (endolymph) and scala tympani (perilymph) in the same animals. At 4 kHz, we found larger electrical responses in the endolymphatic system, requiring 10 dB lower sound level to achieve the criterion 500 μV response amplitude. The difference between endolymph and perilymph increased

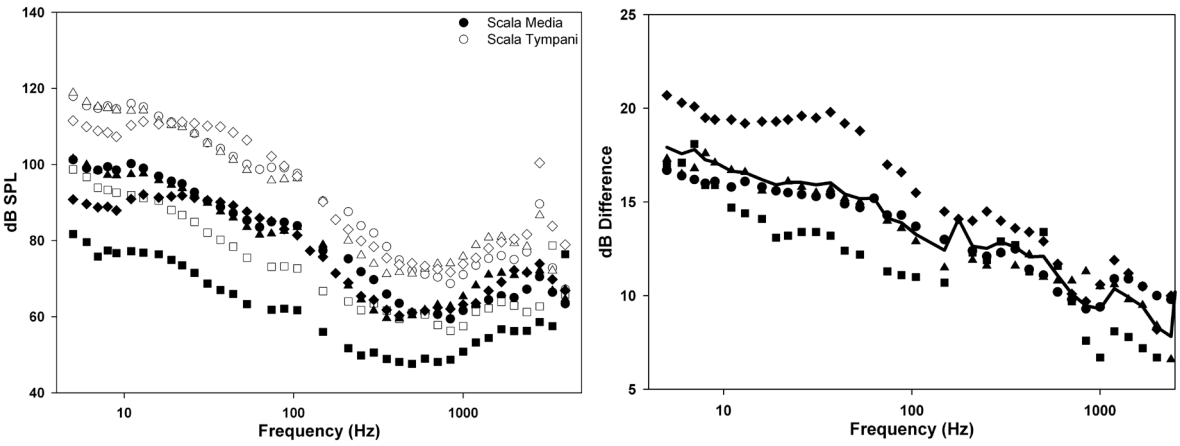

Figure 2: ***Left:*** *Thresholds of stimulation required to generate a cochlear microphonic amplitude of 500 uV in scala media (filled symbols) or scala tympani (open symbols) of the cochlea of 4 animals.* ***Right:*** *The difference between the thresholds measured in perilymph and endolymph. Positive values indicate that larger responses were generated (resulting in lower measured thresholds) in the endolymphatic space (scala media). The cutoff in sensitivity as frequency decreased was lower in the endolymphatic space. This demonstrates that low-frequency sensitivity varies in different parts of the ear, with the endolymphatic space showing relatively higher sensitivity to infrasound. The difference averaged 18 dB at 5 Hz.*

systematically as frequency decreased, with the difference approaching 20 dB at the lower frequencies tested. These measurements show that responses in the endolymphatic system were larger than those measured in perilymph. They vary in a frequency-dependent manner, generating relatively larger responses with infrasound stimulation. Even with the high (500 μV) response criterion, microphonic thresholds measured in the endolymphatic space were in the 80-100 dB SPL range.

2) Inner ear sensitivity to infrasound.

The sensitivity to infrasound was greater when measured in the higher cochlear turns, which predominantly respond to lower frequencies. In Figure 3 we show cochlear microphonic responses evoked from three stimulus frequencies and recorded from the endolymph compartment of the 3rd turn of the guinea pig cochlea. In this experiment, the responses were band pass filtered at the stimulus frequency, and 20 responses were averaged for each measurement to reduce noise levels. Although the ear is less sensitive to 5 Hz compared to 500 Hz (~37 dB higher level required to generate 100 μV at 5 Hz), the maximum voltages generated inside the ear were over 3x greater for 5 Hz (17.3 mV maximum) than for 500 Hz (5.5 mV maximum). This demonstrates that the ear is not only sensitive to infrasonic stimuli, but under some conditions can generate responses to infrasonic stimuli that are larger than those generated for stimuli that are more easily heard by the animal.

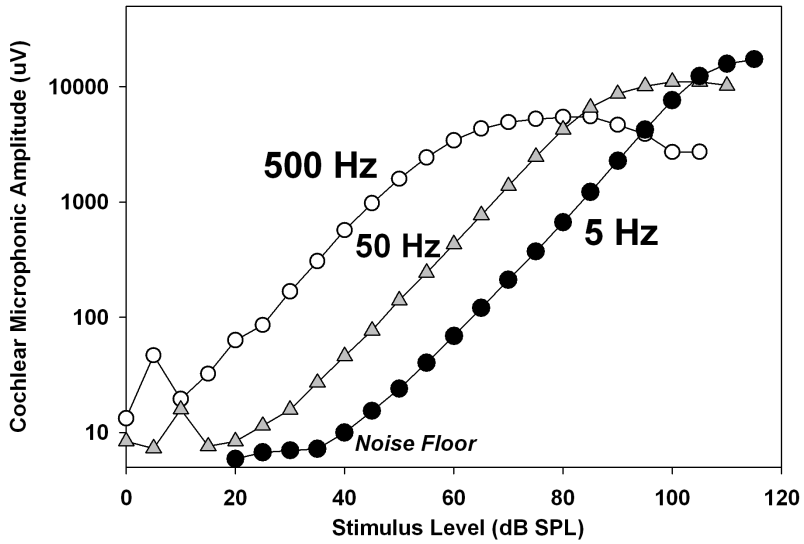

Figure 3: Amplitude of cochlear microphonics recorded from endolymph of the third turn for 3 stimulus frequencies. For each measurement point 20 responses were band-pass filtered and averaged to reduce background noise levels. Although lower sound levels are required to generate responses at 500 Hz, the maximum response amplitude is considerably higher at 5Hz (17.3 mV) than at 500 Hz (5.5 mV).

3) Infrasound responses are inhibited by sounds of higher frequency.

The large potentials generated in the endolymphatic system of the ear in response to infrasound have unique properties that differ from those in response to higher frequency sounds. When two sounds at high-frequency are presented simultaneously to the ear the cochlear microphonic response they generate is typically the sum of the responses to the two signals. This behaviour is analogous to that of a microphone and is the basis of the naming of this response as the cochlear “microphonic”. Thus, at the level of the cochlear microphonic, one sound does not generally inhibit the other. The cochlear microphonic responses to infrasonic stimuli behave differently, however, and are sensitive to the presence of other sounds of higher frequency. In Figure 4 we show an experiment in which a 500 Hz probe tone was superimposed on a sustained 5 Hz stimulus. The recording shows that when the 500 Hz tone was present, the response to 5 Hz was markedly reduced. Analysis of these results shows that the low-frequency response amplitude was initially 8.4 mV peak and was reduced to 2.3 mV peak when the 500 Hz stimulus was present.

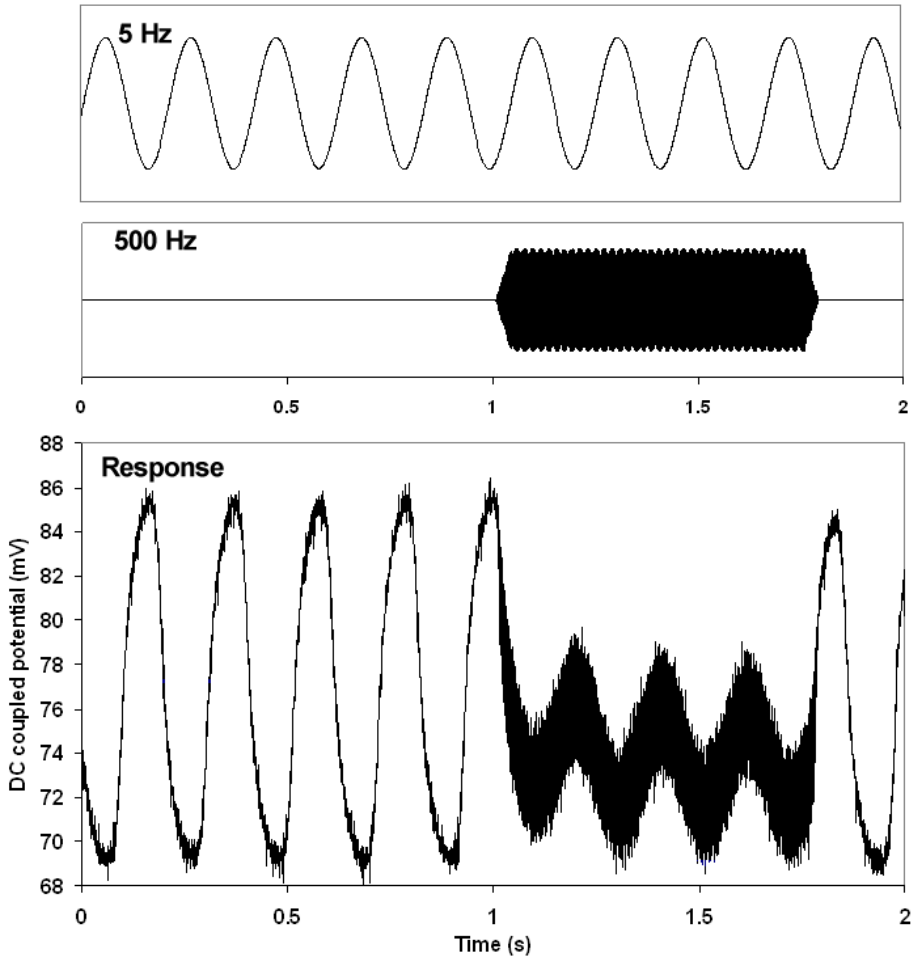

Figure 4: Cochlear microphonic responses from the endolymphatic space of the third turn of the guinea pig cochlea in response to a 5 Hz, 110 dB SPL, 2 s duration stimulus with a superimposed 500 Hz, 80 dB SPL stimulus commencing after 1 s as shown in the upper panels. The cochlear response to the 5 Hz stimulus was dramatically reduced for the duration of the 500 Hz stimulus. Responses were recorded as a single epoch with no averaging.

Although the example demonstrates the phenomenon with a high (110 dB SPL) infrasound level, a similar suppression of the infrasound response occurs with the infrasound at levels as low as 80 dB SPL, as shown in Figure 5. The level of probe tone needed to suppress the infrasound response was approximately 60 dB SPL.

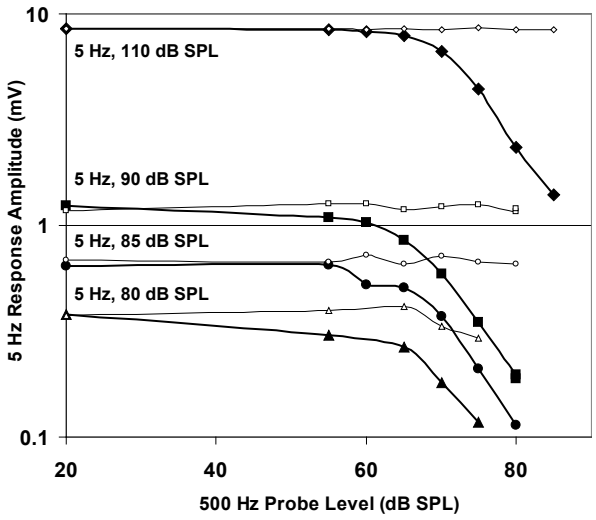

Figure 5: Suppression of cochlear microphonic responses to infrasound (5 Hz) with different levels of the infrasound and of a superimposed 500 Hz probe, as shown in the previous figure. Each curve shows measured responses at the infrasound level indicated. Open symbols show the 5 Hz response amplitude in the region preceding the probe, while solid symbols show the 5 Hz amplitude measured during the probe. Responses to both high (110 dB SPL) and low (80 dB SPL) levels of infrasound stimulation are suppressed by the presence of an audible tone.

4) Responses from the auditory nerve show how a low-frequency sound, that do not by itself excite a single-fiber, can amplitude modulate responses of higher frequency stimuli.

Approximately 30,000 fibers comprise the afferent portion of the cat auditory nerve. We measured single-fiber responses by inserting an electrode made from glass capillary tubing into the region between the ear and the brainstem. When a single-fiber was contacted, we recorded its response with no stimulus (to measure the fiber's "spontaneous rate"), with a high-frequency tone alone, a low-frequency tone alone, and combinations of a probe tone at constant level with a low-frequency tone that was varied in level (Lichtenhan, Guinan, and Shera, 2011). The right panel of Figure 6 shows the firing rate of one fiber under different stimulus conditions. This fiber had a low-spontaneous rate that did not increase (show excitation) when a low-frequency (50 Hz) tone was presented alone. A probe tone of 910 Hz, which was at the "best frequency" for this fiber, caused excitation (firing rate increased to approximately 250 spikes/s). As the level of the low-frequency tone was increased, it suppressed the responses to the higher frequency probe tone, even though the fiber did not respond to the low-frequency tone alone. The left panel of Figure 6 shows single-fiber histograms which demonstrate how the nerve fiber responses synchronize to particular phases of the low-frequency tone when the probe and low-frequency tone were presented together. The 20 ms time interval shown corresponds to one cycle of the low-frequency, 50 Hz tone. At the lowest level of the low-frequency tone (65 dB SPL) the responses are unaffected by the low-frequency and the responses occur uniformly throughout the cycle of the tone. As the level of the low-frequency is increased, it can be seen that not only does the firing rate decrease (as shown in the right panel), but also that the responses predominantly occurred at certain time points in the cycle of the low-frequency tone.

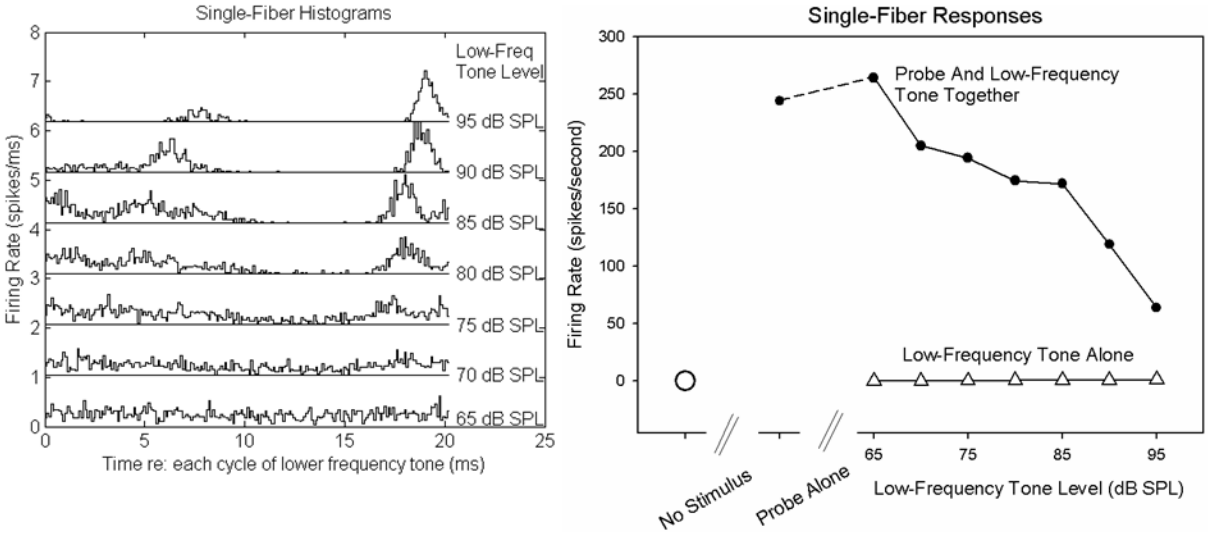

Figure 6: ***Left:*** *A single-fiber's firing rate histogram as a function of one cycle of the low-frequency tone. Here, a higher frequency probe tone (910 Hz – a frequency well above the fundamental frequency of a typical male's voice) and a low-frequency (50 Hz) tone were presented together. As the level of the low-frequency tone is increased, the firing rate is suppressed at particular phases of the low-frequency tone.* ***Right****: The low-frequency tone presented alone does not significantly alter the spontaneous-rate (measured by using no stimulus), while the probe alone did excite the fiber. When a 40 dB high-frequency tone and low-frequency are presented simultaneously, the response from the high-frequency tone is decreased as the level of the low-frequency tone is increased.*

The response of this fiber to the higher frequency tone was clearly modulated by the presence of the low-frequency. These data show that although a low-frequency stimulus, when presented alone, does not excite the fiber (and was therefore not necessarily "heard" by the fiber), the low-frequency stimulus had a marked influence on both the audibility and temporal characteristics of responses to higher frequency signals. This is because although the inner hair cells do not respond to very low-frequencies, they are affected by high-frequency responses of the outer hair cells, which are sensitive to and are modulated by the low-frequency tone

Conclusions

We have presented a number of measurements showing how the inner ear is sensitive to low-frequency and infrasonic sound stimuli presented at levels well below those that would be heard. Our results are consistent with the interpretation that hearing occurs through the inner hair cells which are AC-coupled to the stimulus, while the measured cochlear microphonic responses are generated by the outer hair cells that are DC-coupled to the stimulus. On the basis of these findings it seems reasonable to conclude that when a subject cannot hear a low-frequency sound, this cannot be taken as evidence that the sound cannot affect ear or the subject in other ways.

Our measurements from single-fibers of the auditory nerve show how low-frequency tones that do not by themselves stimulate nerve fibers, can modulate responses to higher frequency stimuli that certainly do stimulate the fiber.

Comparable findings from experiments in chinchillas were reported by Temchin et al., 1997. The frequency dependence they found led them to conclude "that a (high-pass) frequency filter is interposed between the site of origin of modulation and suppression and the site where auditory nerve excitation thresholds are determined". The most likely candidate for this high-pass frequency filter is the sub-tectorial fluid movement that couples outer hair cell movements to the inner hair cells, which in turn provide "hearing". Because the outer hair cell's stereocilia are imbedded in the tectorial membrane, their responses (and their ability to amplify high-frequency sounds) are affected by low-frequency or infrasonic tones while the inner hair cell's stereocilia are not. The inner hair cells can thus "see" the outer hair cells' amplitude modulated, high-frequency output and pass that representation to the auditory nerve which forms the basis of hearing.

This raises the possibility that there are multiple mechanisms by which infrasound or low-frequency sounds, at levels too low to be heard, could influence the representation of sounds in the brain. They can suppress and amplitude modulate responses to higher frequency sounds. By slowly displacing the organ of Corti, they can modulate harmonic distortions to higher frequency stimuli or two-tone emissions (Brown et al., 2009). Such modulation of distortion has been observed both in animals and in humans through acoustic emission measurements from the external ear canal (e.g., Marquardt et al., 2007). The outer hair cells could also stimulate their own afferent innervation directly. The stimulus conditions that cause excitation of the outer hair cell afferents remain largely unexplored. Some have suggested that the afferents may be used in a local network to synchronize the responses of outer hair cells (Thiers et al., 2008). Because these afferents have synapses in the cochlear nucleus of the brain (Benson and Brown, 2004), that central projection could provide an input which may be subconscious.

These findings are relevant to the perception of the "amplitude modulation" of sounds, and represent a biological form of modulation by low-frequency sounds that cannot be measured with a sound level meter. Indeed, some have described how low-frequency biasing can suppress the audibility of higher-frequency tones in the range of speech frequencies (e.g., Zwicker, 1976). A resulting consequence of amplitude modulation of speech sounds by wind turbine infrasound may perhaps be a more difficult, or perceptually taxing, listening environment. Such amplitude modulation of speech sounds may contribute to the "noise annoyance" and problems with "noise sensitivity" reported by Pedersen and Waye (2004)

Responses of the ear to infrasound are substantially greater when measured in the endolymphatic system. The greater sensitivity to infrasound probably results from alterations in ion transport during the relatively prolonged displacements of the organ of Corti during individual cycles of very low-frequency sounds. This is analogous to the voltages change in the battery of a device when sustained current is drawn, compared with those when current draw is modulated (both increasing and decreasing) at high-frequency.

The presence of high-frequency sounds suppresses some aspects of the ear's response to infrasound. This means that under conditions where infrasound levels are high, while ambient sounds are low, the ear may be maximally affected by the infrasound. This may be relevant to the exposure of people to wind turbine sounds in a quiet listening environment (such as a bedroom), where response to the infrasound

may be augmented relative to listening conditions where higher levels of other ambient sounds are present.

We conclude that the ear exhibits a number of complex physiological responses to infrasound stimulation at moderate levels that may exist in the vicinity of wind turbines under some operating conditions. Because the ear is undoubtedly responding to these sounds, it cannot be concluded that infrasound effects on the ear are insignificant because the sounds are not heard. It is therefore premature to assert that long term exposure to wind turbine noise can have no physiological effect on humans.

Acknowledgments

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