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Acoustic pathways revealed: simulated sound transmission and reception in Cuvier's beaked whale (*Ziphius cavirostris*)

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Abstract

The finite element modeling (FEM) space reported here contains the head of a simulated whale based on CT data sets as well as physical measurements of sound-propagation characteristics of actual tissue samples. Simulated sound sources placed inside and outside of an adult male Cuvier's beaked whale (*Ziphius cavirostris*) reveal likely sound propagation pathways into and out of the head. Two separate virtual sound sources that were located at the left and right phonic lips produced beams that converged just outside the head. This result supports the notion that dual sound sources can interfere constructively to form a biologically useful and, in fact, excellent sonar beam in front of the animal. The most intriguing FEM results concern pathways by which sounds reach the ears. The simulations reveal a previously undescribed 'gular pathway' for sound reception in *Ziphius*. Propagated sound pressure waves enter the head from below and between the lower jaws, pass through an opening created by the absence of the medial bony wall of the posterior mandibles, and continue toward the bony ear complexes through the internal mandibular fat bodies. This new pathway has implications for understanding the evolution of underwater hearing in odontocetes. Our model also provides evidence for receive beam directionality, off-axis acoustic shadowing and a plausible mechanism for the long-standing orthodox sound reception pathway in odontocetes. The techniques developed for this study can be used to study acoustic perturbation in a wide variety of marine organisms.

1. Introduction

The cephalic anatomy of toothed whales is marked by structural complexes that have long been recognized as components of a sophisticated biosonar system. This sonar system has three categorical divisions: the sound generation and transmission apparatus, the sound reception and transduction apparatus and the central nervous system components that control output and interpret input. The current paper will present results that touch upon the first two categories.

Several structures within the odontocete head are involved in the production or reception of biosonar sounds (Cranford and Amundin 2003). The nasal apparatus in all odontocetes, as compared to all other mammals, is greatly enlarged, fitted with specialized lipid organs, and a set of skull bones that form an amphitheater-like shape. The melon is composed of fatty tissues; it occupies the amphitheater-like face of the skull

and acts as an acoustic channel and an impedance matching device for sounds propagating out of the head (Cranford and Amundin 2003). Current understanding of the structure and function of the odontocete nasal complex is based on data from a taxonomically diverse handful of species.

The sound generation and transmission apparatus is composed primarily of structures that are nasal in origin. The comparative anatomy of this region has been studied in some detail across the entire odontocete suborder (Norris *et al* 1961, Norris 1964, Schenkkan 1973, Mead 1975, Heyning 1989, Cranford *et al* 1996, Cranford 1999). Only in recent years have we been able to ascertain the site and generation mechanism for sonar signals in bottlenose dolphins (Cranford 2000, Cranford and Amundin 2003). It is unclear whether or not other odontocetes are using homologous structures and similar means but it is at least reasonable based on overall structural similarities (i.e., all odontocetes have a similarly telescoped skull; a fatty melon or its homologue; and two pairs of phonic lips with their associated tissue complexes, except for the special case of the sperm whale). For reviews see Cranford (1992), Cranford *et al* (1996) and Cranford and Amundin (2003).

The sound reception apparatus (sound channels and ears) is located along the ventral aspect of the skull and is associated with the mandibles. With respect to understanding odontocete echolocation, one of the most important questions to answer is: Where does sound enter the head of odontocetes and how does it reach potentially vulnerable structures within the hearing apparatus? This seemingly simple question has not been adequately addressed for any odontocete.

The lower half of the head contains the mandibles, specific masses of acoustic fat associated with sound reception, air-filled pterygoid sinus and the bony ear (tympanoperiotic) complex. There is a long-standing notion that sound enters the odontocete head through a structure known as the 'acoustic window' (Norris 1968), a fat body overlying the posterior portions of the lower jaws, after which it traverses the jaw and enters the internal mandibular fat body on the way to the bony ear complex. This idea, also known as 'jaw hearing', is based primarily upon anatomy (Norris 1964, 1968, 1969) and a group of psychoacoustic experiments exemplified by Brill and Harder (1991), who placed a neoprene hood over the jaws and throat region of a bottlenose dolphin (*Tursiops truncatus*) to exclude sound. They reported a severe degradation in echolocation ability with the application of the hood.

Hearing is the culmination of a set of complex processes. In odontocetes, it involves a directivity index that is frequency dependent and structurally mediated; filtering, focusing and transduction, which are also structurally mediated; and central nervous system processing. Most of what we know about hearing in odontocetes is the result of study and experimentation with a single species, the bottlenose dolphin (*Tursiops truncatus*). Any extrapolation from the results of work with *Tursiops* to other species should be undertaken with trepidation, particularly as one proceeds farther afield taxonomically. At the same time, similar results between disparate species may indicate that a common structure/function paradigm is at work or it may argue for convergent evolution mechanisms.

The pathway of sound to the hearing apparatus (tympanoperiotic complex) is the major thrust of this paper. Our studies indicate that the notion of jaw hearing needs refinement, particularly in light of applicable results from the literature. We will also report preliminary results regarding beam formation for sounds transmitted from the animal, as well as another failed test of the laryngeal phonation hypothesis (see review in Cranford and Amundin (2003)). These additional results also bear upon the process of model validation.

Our FEM studies provide a window into structurally mediated processes, which result from the complex interactions between sounds and anatomy. We can, for the first time, model and simulate acoustic pathways in odontocetes. The majority of prior acoustic research into odontocetes is based upon the end result of complex functions as a whole, rather than isolating various aspects of it. The application of FEM allows us to ask questions that consider systems of structures or their isolated contributions. It also provides a means to manipulate the characteristics of structures or systems of structures and conduct virtual experiments to tease apart the contributions to the overall behavior of the acoustic components. Some of these experiments are underway and will be reported elsewhere.

2. Methods

This study capitalizes on the recent availability of industrial CT scanners to collect data from postmortem whales. Over the past 10 years, one of us (Cranford) has developed and tested a technique to scan large cetacean specimens (Cranford 1999). Once obtained the CT scans can be applied to a wide variety of research questions. Foremost among them is the current effort to advance understanding of the interaction between sound and the anatomy of a whale. We have combined the anatomic geometry obtained from industrial CT scanners, tissue property measurements and custom FEM software ('Vibro-acoustic Toolkit') to produce the 'Vibro-acoustic Simulator' (VAS) (Krysl *et al* 2006, 2007), which simulates sounds and their propagation pathways into and out of the specimens represented by these scans.

The heads of two specimens (one neonate female and one adult male) of *Ziphius cavirostris* were frozen to preserve tissue quality, placed in registration frames, and scanned using X-ray CT. After scanning, the specimens were thawed, photographed and dissected. The use of frozen and thawed tissue in anatomy and acoustic studies was supported by McKenna and her colleagues (McKenna *et al* 2007). The neonate female was CT scanned a second time after being thawed. During dissection the tissues were sampled so that the physical properties (sound velocity and elasticity) could be measured, as reported by Soldevilla and her colleagues Soldevilla *et al* (2005). The elasticity values along with the density information given by the scanning process were incorporated into functional/geometric models of the whales' heads. We were unable to measure the tissue properties in the adult male so the values for the elastic properties in the neonate were also applied to the tissues in the adult male model. The

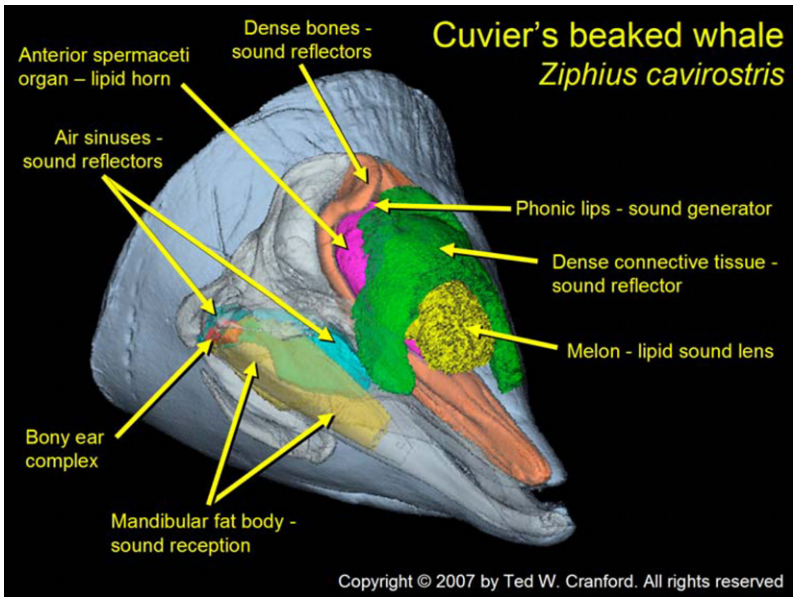

Figure 1. This is a pseudo-3D view of the major components of the biosonar system in *Ziphius cavirostris*. The melon (yellow) is a fat and connective tissue organ that conducts the sound beam out of the head. The sound generation process begins at the phonic lips, located at the posterior extent of the anterior spermaceti organ (magenta), tucked under the overhanging high-density nasal bones forming the prenarial basin (red) of the skull (ivory). Another component of the beam formation apparatus is the dense connective tissue arch (green). The components of the sound reception apparatus are nestled medial to the mandibles: the mandibular fat body (yellow), the pterygoid sinus and the peribullary sinus (cyan), and the bony ear complex (red). The hyoid bones (ivory) hang down below the jaws in the image.

tissue properties can easily be changed in the VAS and we will test the effects of changing them in future work. The results of prior work (Aroyan *et al* 1992) suggest that changing the tissue properties by as much as 10% has little effect on the resultant propagation model but we will investigate this idea further.

We have developed a comprehensive formulation for vibro-acoustic problems in medicine and biology and placed it in the context of a 'toolbox', the vibro-acoustic toolkit. In order to address the difficult problem of discretizing anatomic geometries, the mesh is voxel based, and is generated automatically from common biomedical data sets (CT scans and MRI). The vibro-acoustic toolkit implements a fully Lagrangean finite element formulation based on the decomposition of incident and scattered fields that has been developed to incorporate seamless coupling of fluids and viscoelastic solids, and to allow for accurate representation of incident acoustic excitation (Krysl *et al* 2007).

The propagation of the mechanical (acoustic) disturbance in biological tissues is simulated with the finite element method using the concept of lumping. The inertial effects are accounted for by lumping the distributed mass into point-like particles; the interaction of these particles with each other through the intervening material is accounted for by lumping the elastic and viscous resistance of the material. This produces linkages between the particles through 'springs' reacting to differences in displacement or differences in velocity between the particles.

Our approach is based on the superposition principle and is described in detail elsewhere (Krysl *et al* 2007). The computational model has been verified on common fluid–structure acoustic interaction benchmarks: step-wave interaction with a hollow thin-walled cylinder and scattering from an elastic solid sphere (Krysl *et al* 2007). The displacement field (vector function with three components of displacement along each Cartesian axis) is split into the incident field (known, typically corresponding to a planar or spherical sound wave in the infinite fluid medium in which everything is embedded), and the disturbance (perturbation) field (unknown; it is due to the presence of other fluids or solids, or cavities in the infinite surrounding medium).

The 3D space or 'model space' in which the simulations take place can be imagined as an elongate square column containing the centered head of an adult male *Ziphius cavirostris*, where the remaining space outside the head is filled with sea water. In the model, simulated sound sources can be placed inside of the head or outside of it in the sea water. Most of the simulations used a constant frequency signal at 40 kHz because the echolocation signals recorded from these animals in the wild are narrow-band with a 40 kHz peak frequency (Johnson *et al* 2004, Zimmer *et al* 2005). We also simulated short-duration impulse signals.

3. Results

The first simulations began with sound sources in the head at the phonic lips, known to be the source of sonar signals in the bottlenose dolphin (Cranford and Amundin 2003). The forehead anatomy in *Ziphius cavirostris* (figure 1) and *Tursiops truncatus* is based upon similar basic structural outlines (Cranford 1992, McKenna 2005). If a forwardly

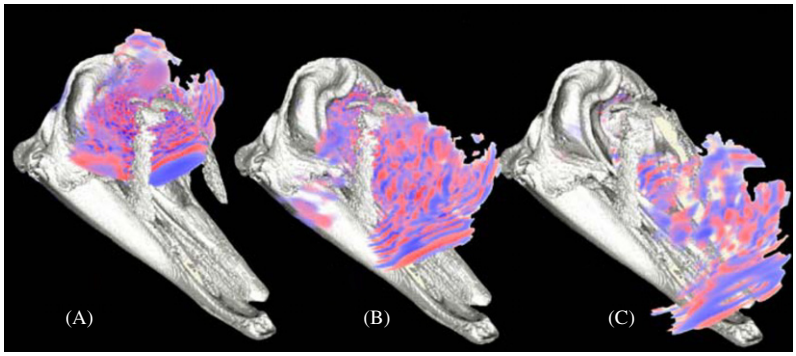

Figure 2. Formation of a forwardly directed sound transmission beam. Three frames from a simulated 40 kHz sound source at the right phonic lips. All of the anatomy was used in the simulation but most of the anatomic structures were made transparent for rendering these frames in order to show the emerging beam. The skull, mandibles and connective tissue arch remain opaque in order to orient the reader. Red indicates positive sound pressure and blue is negative sound pressure.

directed sound beam was generated in the simulations (as has been measured in *Tursiops* and a few other odontocetes) then these first simulations can be seen as a basic validation of the model and methods. The sound beams generated were directed forward and collimated somewhat by the structures along the propagation pathways (figures 1 and 2).

Building, testing and refining the vibro-acoustic simulator (VAS) is an iterative process that relies on validation, and feedback. The results reported here should be seen as emanating from a snapshot in that iterative process.

3.1. Overlapping sound transmission beams

A simulated sound source placed at the phonic lips to the right of the nasal septum (figure 1) produces a beam that emerges from the head after being formed into regular wavefronts (figure 2). A source placed at the complimentary location, the phonic lips to the left of the nasal septum, also produces an acoustic beam with its center axis emerging from the head along the midline. The beams produced from simulated sound sources at the left and right phonic lips overlap in front of the head along the horizontal axis. In our simulations, some of the energy in the forwardly directed beam refracts around the tip of the mandibles, ventrally, and winds up in front of the mouth.

Figure 3 shows that the outgoing signal is different inside the melon than it is just outside the head at the tip of the nose. Note the similarity between the signal at the tip of the nose and one recorded from *Ziphius* in the wild.

3.2. Laryngeal sound source not supported

A significant volume of the early literature contains a debate about whether odontocete biosonar signals, such as most mammal sounds, were generated in the larynx or in the nasal apparatus. Originally, it was assumed that the source of odontocete sonar signals was located in the larynx. The 'laryngeal phonation hypothesis' was put forward largely based on anatomic evidence, sparking a debate that raged in the literature for two decades (reviewed in Cranford (2000) and Cranford and Amundin (2003)). Experimental evidence called this notion into serious doubt beginning in the 1980s (Ridgway *et al* 1980). The bulk of research in the intervening years does not support the laryngeal phonation hypothesis (Cranford and Amundin 2003). We tested the laryngeal phonation hypothesis in *Ziphius* using the VAS and found that a sound source placed at the tip of the larynx does not produce a forwardly directed beam, rendering it improbable as a biosonar source.

3.3. Multiple sound reception pathways

How or by which pathways does sound reach the hearing apparatus? The answers to this question are important for understanding the function of odontocete echolocation as well as potential impacts from exposure to anthropogenic sound.

3.3.1. The 'old' or conventional sound pathway. The conventional sound reception pathway for odontocetes is known by the colloquial term, 'jaw hearing', first put forth by Norris in 1968. A detailed study of mandibular structure led him to propose that sound entered the odontocete head through a fatty pad, the 'acoustic window' (Norris 1968, 1974). This fat pad lies between the skin and the thin posterior portion of each mandible or 'pan bone'. Odontocete mandibles are hollow and the medial bony wall or lamina is absent. These mandibular cavities are filled with pellucid fat bodies. These internal mandibular fat bodies extend posteriorly to form a channel and attachment to the bony ear complexes (tympanoperiotic)[4]. According to Norris, sound passes from the acoustic window through the thin external bony lamina of the pan bone and propagates along the internal mandibular fat body to the tympanoperiotic complexes.

There have been several studies that have attempted to validate or discount Norris' jaw hearing hypothesis (see review in Ketten (2000)) but a mechanism for how sound traverses the pan bones has never been proposed.

We tested the jaw hearing hypothesis with the VAS. These findings indicate that jaw hearing requires a specialized

[4] The fatty channels are ubiquitous to all odontocetes but the chemical composition of those lipids depends upon taxonomy (Koopman *et al* 2006).

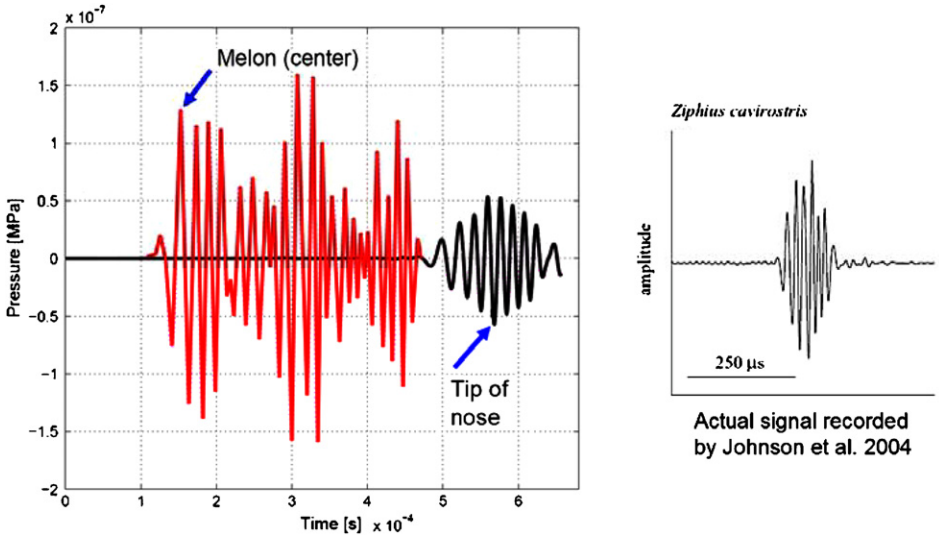

Figure 3. Acoustic signals that are transmitted through the head are apparently shaped by the propagation pathway. In the above case, the initial signal in the simulation began at the phonic lips on the right (Cranford *et al* 2008) and used an initial velocity applied radially to a small volume in the form of a hill function (See Krysl *et al* (2007)). Two virtual receivers recorded the output during the same simulation, one from within the mid portion of the melon and the other just outside of the head near the tip of the rostrum. The dramatic difference between the model signal sampled from within the melon and that at the tip of the nose indicates that significant shaping or conditioning of the signal occurs along the sound propagation pathway. We can also see that the signal at the tip of the nose looks remarkably similar to a signal that was recorded from *Ziphius cavirostris* in the wild (Johnson *et al* 2004) (Reproduced by permission).

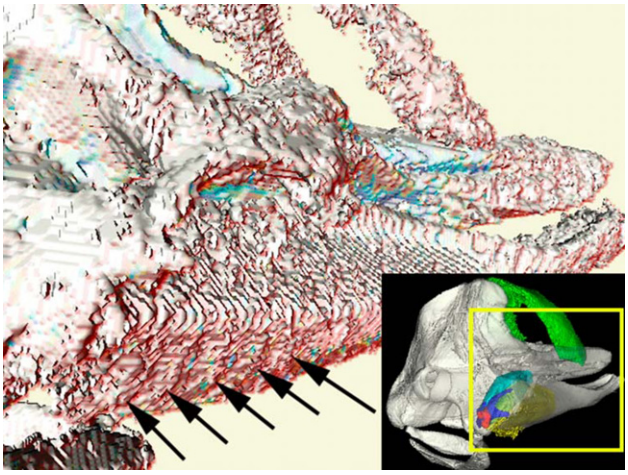

Figure 4. The FEM tools suggest that a flexural wave in the mandibles may explain the mechanism of the 'jaw hearing' theory in odontocetes (Norris 1968). The main part of the figure above is from a simulation where the sound source was 40 kHz, and 0° elevation above the horizontal. The inset image at the lower right shows a context image and a frame that approximates the view seen in the simulation at the left. In the simulation, the flexural wave peaks are indicated by the black arrows and can be seen traveling posteriorly along the jaw. These waves have been exaggerated for the purposes of visualization.

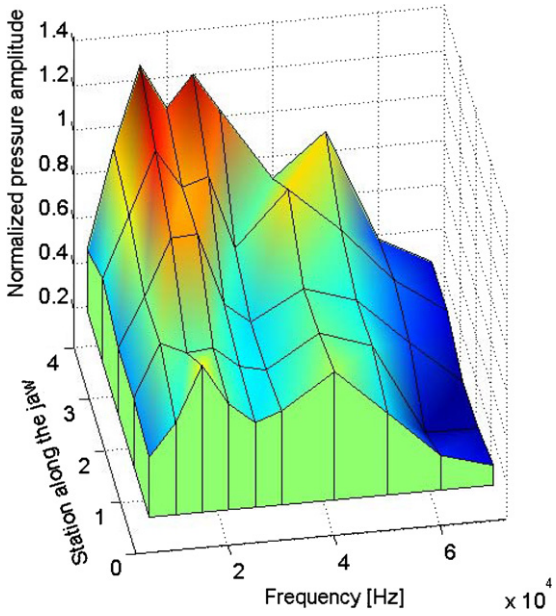

Figure 5. Efficiency of pressure transmission through the mandible as a function of frequency. This graph shows the normalized pressure amplitude along the jaw as a function of frequency. Pressure peaks occur near 20 kHz and 40 kHz at posterior stations of the lower jaw and the efficiency rises posteriorly (stations 0–4).

mechanism to account for sound passing through bone. Simulated sound waves that are incident upon the jaws within specific angles of attack (i.e., from in front of and slightly to one side or the other of the animal) produce a series of small amplitude waves that flex specific regions of the pan bone of the mandible (figure 4). This flexural wave mechanism for jaw hearing is the first explanation for how sound crosses the pan bone.

Figure 5 shows the result of a parametric study that computed the pressure amplitude at various stations along the interior jaw for vibrations transmitted exclusively *through*

the jaw. The parameter is the frequency of the incident planar harmonic acoustic wave. The graph shows the pressure amplitude at a series of stations along the pan bone (anterior to posterior, where station 0 is the point where the mandible becomes single-walled anteriorly, and station 4 is at a point near the temporomandibular joint, where the jaw is joined to the skull). The pressure is normalized by the amplitude of the incident pressure wave at infinity. Note that the amplitude of the pressure wave on the outside of the mandible is typically much higher (about 1.5 to 2 times higher) than the amplitude of the incident pressure wave at infinity. Therefore, the normalized pressure amplitude measured in the interior and equal to 1 means that the mandible is 'transparent' as a measure of how much the mandible limits the transmission of sound pressure between the outside and the inside. Since the amplitude of the pressure acting on the mandible from the outside is typically higher than the amplitude of the incident pressure at infinity, the efficiency may be higher than 1. The presence of the mandible creates a pressure perturbation (essentially boosting the pressure amplitude both on the inside and outside). On the other hand, it also causes reflections which shield the interior from the incident pressure. If these two effects are balanced, the efficiency is 1, and the jawbone may be considered 'transparent'. If the shielding prevails, the measured amplitude on the interior is lower than the incident pressure; otherwise, the effect of the pressure boost is bigger than the shielding and efficiency greater than 1 may result.

Two large peaks occur near 15 and 40 kHz (figure 5) after which the normalized pressure drops off precipitously. These peaks indicate that the mandible becomes increasingly transparent posteriorly.

3.3.2. The 'new' sound pathway. In addition to the conventional notion of jaw hearing, our studies indicate that sound reception may also occur by way of the oral cavity and gular region (figure 6). In this example, a simulated 40 kHz planar pressure (p) wave approaches the animal with an angle of incidence of 0° (i.e., horizontal). When the acoustic pressure wave encounters the cone of soft tissues surrounding the head, it refracts around, largely below, and between the mandibles enters the internal mandibular fat bodies through the opening created by the absence of the medial bony wall of the mandible and propagates caudally to the bony ear complex (figure 6). This acoustic pathway to the ears has not been adequately considered. We will refer to this sound reception pathway through the oral cavity and gular region as the 'gular pathway'.

The intensity of the p waves that reach the bony ear complexes are dependant upon angle of incidence, in both the horizontal and vertical planes. For example, if the sound source is placed outside of the head and slightly to the left of the head on the horizontal, the signal reaches the right ear with some time delay (∼100 μs) and diminution (∼6 fold) in intensity (figure 7).

Alternatively, if the sound source is located along the vertical midline axis and is then raised above or lowered below the horizontal, the intensity of the received signal is diminished equally at both ears (figure 8). Frequency filtering, if it occurs along the new gular pathway, is not immediately obvious and will be the subject of future investigations.

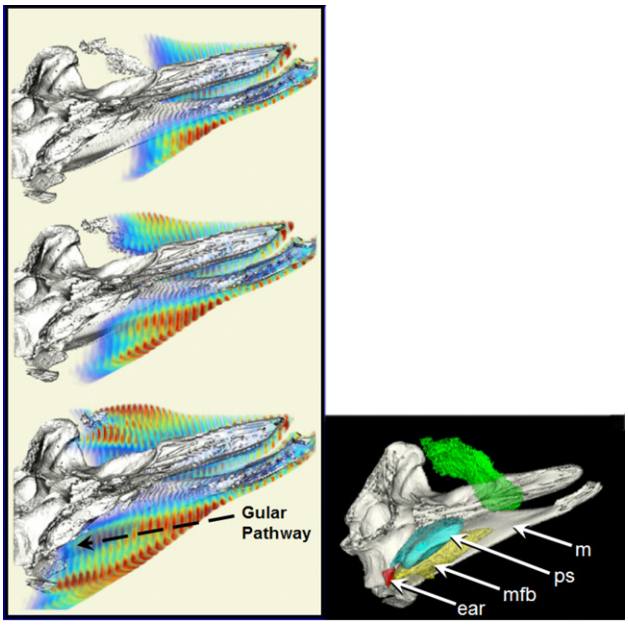

Figure 6. Three frames from an FEM simulation showing the displacement amplitude. In this case, a 40 kHz planar wave was incident upon the specimen from directly in front and 0° above the horizontal. In order to facilitate viewing of the propagation process, the right side of the specimen was removed and only high density structures are displayed during the rendering of the movie frames. But the original simulation included the entire head and all anatomic components. This new 'gular pathway' is shown by waves that refract or wrap around the ventral margin of the mandible, enter the fatty channel on the inside of the mandible and propagate back to the bony ear complex. The inset shows the anatomy that would be found in the simulation frames if it had not been removed to facilitate viewing. The view is of the left side of the head, as viewed from the right. The inset image is reconstructed from CT scans and shows a few important sound reception components, labeled (ear = left tympanoperiotic complex; mfb = left mandibular fat body; ps = left pterygoid sinus; m = left mandible).

4. Discussion

4.1. Sound transmission beams

The mechanism for producing a sound beam is undoubtedly complex and involves contributions from several anatomic components. Figure 3 demonstrates that the signal is 'shaped' or 'conditioned' by the various structures along the propagation pathway. This sort of result can only be discovered by using FEM methods. Fortunately, future studies can take advantage of the flexibility of the simulator, such that the properties of various structures can be changed systematically and the simulation results compared to extract the contributions of the various components.

Of the various components, the pachyosteosclerotic elements of the skull ('Dense bones' colored red in figure 1) apparently play an important roll. There is also a part the sound transmission pathway that includes a large fat body (anterior

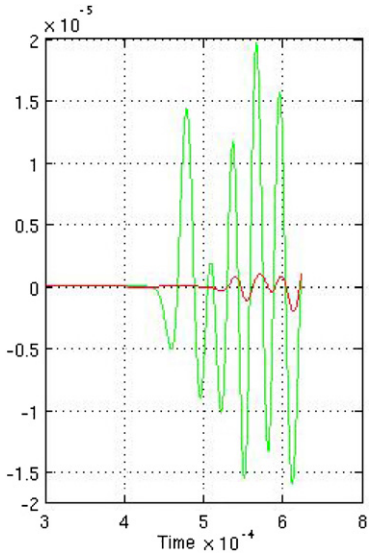

Figure 7. Acoustic shadowing. These records of time versus relative amplitude indicate that there is a time delay and an amplitude diminution in acoustic pressure with respect to each tympanoperiotic complex. In this case the simulated sound source was placed in front of the animal at 0° above the horizontal and less than 2° to the left of the midline. The green trace shows that the acoustic pressure wave arrives earlier in time and at higher amplitude at the left ear than at the right ear. The red trace demonstrates that a collection of anatomic structures shield the right ear complex from sounds that come from sources to the left of the midline.

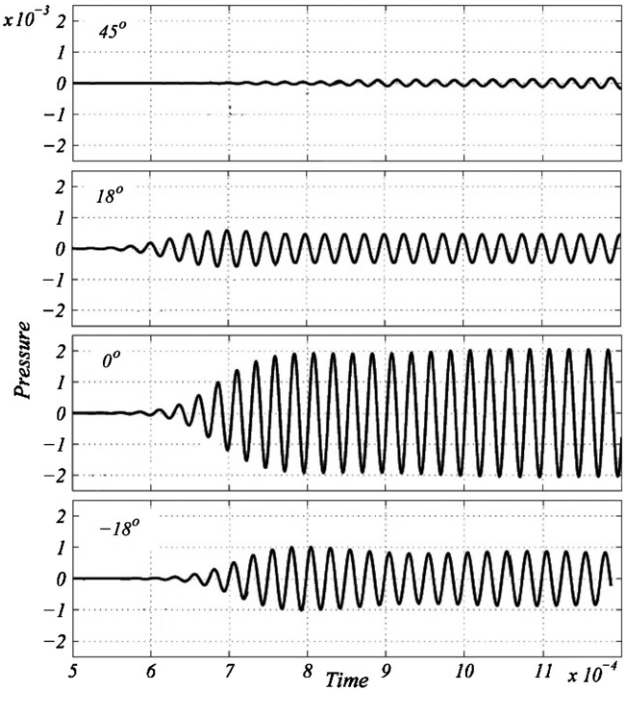

Figure 8. This panel shows that sound pressure amplitude arriving at the left tympanoperiotic complex decreases as the simulated on-axis sound source is moved above or below the horizontal. The lowest intensity arrives from a planar wave that arrives from 45° above the horizontal. The highest intensity arrives from 0° in the vertical plane, i.e., from the horizontal. The abscissa is marked in fractions of a second. The ordinate indicates the relative amplitude.

spermaceti organ) immediately ventral to the melon that is unique to *Ziphius* (figure 1). These anatomic components, and especially the geometry (shapes, sizes and relative interfaces) among the components, are important in the production of a sonar beam (Cranford *et al* 2008).

Readers might be reasonably concerned about the values we have used for tissue elasticity in the model since the gross scale of the samples (Soldevilla *et al* 2005) is not as refined as the scale of the density map given by the CT scans (Cranford *et al* 2008). If there are mistakes in the representation of the tissue properties, it appears that they are relatively small because the simulation results given by figures 2, 3, 7 and 8 are what we should expect considering prior work on a wide variety of odontocetes. Aroyan *et al* (1992) used tissue property values from the literature, gleaned from measurements of various mammalian tissues and produced a simulated transmission beam that approximated those reported in the literature for dolphins. They also reported that changing tissue properties by 5%–10% had little effect on the resultant beam geometry in a CT-based model of *Delphinus delphis*. This notion that the geometry of tissue structures and their interfaces are more important factors in beam formation than any small variation in tissue properties is also supported in our *Ziphius* simulations. For example, in a few probes where we changed the stiffness of the bones up or down by 10% there was no change in the resultant beam shape or direction, but when the stiffness was lower, more energy propagated into the bones. Of course, another possible explanation for answers that approximate reality in a model is that it results from multiple mistakes that cancel one another. This is a possibility that we are always aware of and guard against by constantly checking new results against those from live animal systems.

Independent simulations with sound sources located at the left and right phonic lips produce beams that overlap just outside the head. These results support the notion that sounds generated from two sources (one at each set of phonic lips) may interfere constructively to form a biosonar beam in front of the animal (Cranford and Amundin 2003). This is consistent with current understanding of the biosonar system in the bottlenose dolphin, where left and right phonic lips can operate independently or simultaneously to produce a transmitted sonar beam (Cranford, personal observation).

The simulated beam patterns produced by two sound sources are also consistent with the results obtained by Zimmer and his colleagues (Zimmer *et al* 2005) for free-ranging *Ziphius*. They report that most of the echolocation signals emanate from or near the central axis of the animal's body, normally within 40° of that axis. In our simulations, sound sources placed at either one of the phonic lips locations produced a forwardly directed beam whose axis was near the midline. These results are similar to what has been described for other odontocetes, *Tursiops truncatus* (Au *et al* 1986), *Pseudorca crassidens* (Au *et al* 1995), *Delphinapterus leucas* (Au *et al* 1987) and *Phocoena phocoena* (Au *et al* 1999, 2006), all produce acoustic beams that are similar in shape and direction.

With respect to the beam axis results and the observations of Zimmer and his colleagues, the questions become: Is the

beam axis static in direction with reference to the body axis or can the animal vary the direction of the beam axis? In other words, do these animals have the ability to steer the beam axis, and if so by what means and to what degree?

It is possible that two independent and spatially separated sound sources could be actuated with differing phase relationships to produce a variable beam trajectory or 'beam steering', a function that has also been proposed for non-physeterid odontocetes (Cranford and Amundin 2003). Sonar beam steering has been suggested in harbor porpoises (Amundin 1991) and it has long been suspected for other odontocetes but this question awaits focused investigation. The notion that odontocetes can change the acoustic beam geometry has been measured in the sperm whale (Møhl *et al* 2000). Currently we cannot simultaneously activate two sources within the model space to test the idea of beam steering by phase shifting the sources and interference but are adding these tools to the vibro-acoustic toolkit so that we can address these questions in future studies.

Collectively, the characteristics in the simulated transmission beam and the close approximation to results from studies with live free-ranging animals (Zimmer *et al* 2005) suggests that the collective results from our work with the VAS passes a basic test of validation for the adult male *Ziphius*.

4.2. Sound reception pathways

The gular sound pathway into the ears described herein is a discovery that now seems somewhat conspicuous considering that it provides a virtually an unobstructed path to the hearing apparatus. Norris and Harvey (1974) anticipated that some sound reception might occur through the mouth and throat, particularly when the animal closes in on a target. They did not, however, suspect that the gular pathway might be the primary pathway for sound reception.

There are a couple of 'odd' or isolated lines of evidence in the literature that suggest the gular pathway is functional in the bottlenose dolphin. Møhl and his colleagues Møhl *et al* (1999) reported that the *most* sensitive region for sound entering the head was slightly forward of Norris' acoustic window. Curiously, they also noted a region of high (acoustic) sensitivity along the ventral midline in a bottlenose dolphin (essentially as high as the greatest sensitivity measured), but they did not otherwise comment on this interesting result. We surmise that this unique result for *Tursiops* supports our preliminary results for *Ziphius*, implying broad taxonomic distribution.

If the gular pathway is valid it could only function in the absence of the medial bony lamina of the posterior portion of the mandible, a condition that exists in all toothed whales and their ancestral archaeocetes. Since the medial bony wall is absent in all known odontocetes, we speculate that this gular pathway is functional across the suborder. At the same time, the outer walls of the posterior mandibles in archaeocetes are relatively thick, unlike extant odontocetes, so it may be that the flexural wave mechanism was not functional in the ancient whales. Perhaps the primordial underwater hearing pathway in whales was through the gular region and that jaw hearing was a more recent development.

A technical report (Brill *et al* 2001) found high sensitivity when their 'jawphone' (composed of a suction cup coupled to a hydrophone) was placed slightly anterior to the acoustic window. Unfortunately, they had difficulty maintaining the suction cup attachment of the jawphone at a location on the ventral (gular) side of the head. The work by Brill, Møhl and their colleagues (Brill and Harder 1991, Møhl *et al* 1999, Brill *et al* 2001) clearly supports the jaw hearing hypothesis of Norris (1968) but the mechanism for the transmission of sound across the bony wall of the mandible remains unresolved.

Our FEM simulations suggest that the thinned posterior walls of the lower jaws are forced into a series of flexural waves by incoming sounds, provided that the sounds and bone have a specific set of characteristics. This is one possible explanation for the mechanism of jaw hearing but it is complex and by no means certain. As it turns out, the theoretical basis of this idea had apparently already occurred to Møhl and his colleagues Møhl *et al* (1999). Considering our findings, the comments they made in the last paragraph of their discussion seem prescient:

> 'When evaluating the models, it should be borne in mind that the cross section of the mandible is on the same order of magnitude as the dominant wavelength of *p*-waves (compressional or longitudinal waves, as opposed to transversal and shear waves) in water and soft tissues at 50 kHz (3 cm). A logical consequence of this observation is that models inspired from optical analogies (reflections, refraction, etc) are problematic, as they require structures that are considerably larger than the wavelength. However, in mixed media with solid components, other sorts of waves than compressional, longitudinal ones can be realized'. (Møhl *et al* 1999, p 3424)

Their proposition that combinations of wave types are likely to be operational in mixed media containing solid components, is directly in line with what we see in the VAS simulations. The new gular pathway certainly does not negate Norris' jaw hearing pathway but it does change our understanding of it. One explanation of the flexural wave notion is that pressure (P) waves incident upon the mandibles are translated into P waves and shear (S) waves in the thin posterior bony shell, the pan bone, of the mandible or lower jaw. That this combination (P&S) wave may be in phase with the wave incident upon the mandible to form flexural waves within the thinned pan bone is supported by our simulation results and the assertions of Møhl *et al* (1999). Once the P waves and S waves create flexing in the thin bony wall the sound will propagate into the internal mandibular fat bodies and through them to the bony ear complexes.

The flexural wave mechanism is admittedly complex and there is much work ahead to test the veracity of this proposal. This mandibular mechanism depends upon a number of factors including the geometry and elastic properties of the mandibles and adjacent soft tissues as well as the acoustic frequency and its angle of incidence. There is an indication that the flexing is accentuated by interference between successive pressure

wavefronts reflected from the bones, such that the waves gain amplitude as they travel caudally, resulting in areas along the jaw bone where the pressure is greater than the pressure of the incident planar wave before it reaches the rostrum (figure 5).

Figures 4 and 5 support the flexural wave notion of sound transmission across the mandibles and buttress the case for Norris' acoustic window. Since transmission by this mechanism depends on the elastic properties of the bone, those properties should be measured explicitly for odontocete mandibles. The flexural wave mechanism requires us to sort out a complex set of intermingled physical parameters, a process that is already underway.

One question that arises from the flexural wave proposal involves the possibility that sound transmission through the mandible functions as a kind of 'tonotopic' frequency filter, allowing selected frequencies to pass at certain locations and blocking others. Is there a comparative or discriminative value between sounds arriving via the two pathways (i.e., jaw hearing and gular pathways)? We can conceive that the flexural wave mechanism could cause filtering to occur by preferentially passing frequencies according to the thickness of the bony wall and various other properties of the bone. Norris (1968) has shown that 'C' shaped cross sections of the mandible change gradually in thickness along its length and may therefore pass certain frequencies (e.g., filtering) according to the parameters of mandibular structure and the acoustic signal incident upon it.

In 1984, Au and Moore published the received beam patterns for two bottlenose dolphins using psychoacoustic methods (Au and Moore 1984). The pattern they reported is similar to that shown in figure 8, where the highest sound pressure amplitude received at the ears arrives from directly forward of the rostrum and the received amplitude drops off above and below the horizontal plane. The congruity between the Au and Moore results and our simulations suggest a similar pathway in representatives from vastly different taxa. It is somewhat counterintuitive that a planar sound wave arriving from below horizontal (-18° in figure 8) reaches the ear with a lower amplitude than one arriving from the horizontal. It seems reasonable that sounds originating from below the horizontal axis should have direct and unfettered access to the gular pathway, yet our results and those of Au and Moore (1984) suggest that this is not the case. This evidence suggests that the gular pathway may have a receive beam directivity index and that the mechanism might be generalizable to all odontocetes. Our toolkit should allow us to tease apart the anatomic basis of this mechanism.

The VAS can also use to predict changes to acoustic waveforms at any point in the simulation space as a result of the complex interactions among other structures within the head. Our simulations allow us to predict the time delay and the difference in amplitude between signals that reach the ear complexes from a sound originating in front of the head and off-axis laterally (figure 6). These interaural differences are apparently due in large part to shielding by a suite of anatomic structures. Specifically the juxtaposition of the large pterygoid sinuses, a fibrous venous plexus and lipid-rich pathways that connect the acoustic environment to the bony ear complex provide a means for understanding and delineating the specific contributors to interaural differences. It may be that the time delay, phase differences, or amplitude differences between the gular pathway and jaw hearing pathway provide additional acoustic cues to the animal during biosonar. We will address these questions in future investigations.

These results demonstrate a powerful combination of techniques that provide a reliable, low-cost tool that can be used to investigate questions that probe the interaction between anatomic structure and a limitless choice of sound sources. The value of this technological innovation increases with the taxonomic expansion of the digital library of cetacean anatomy. Finite element modeling facilitates investigations of acoustic exposure across a broad spectrum of species, including non-mammalian aquatic vertebrates.

5. Conclusions

The vibro-acoustic simulations presented here suggest a new acoustic pathway to the ears from around and under the mandibles and that a flexural wave offers a plausible explanation for the conventional pathway through the thinned mandibles as originally described by Norris (1968, 1974).

The fact that a source placed at either of the phonic lip locations produces a narrow, forwardly directed beam leads to plausible functional explanations. These sound transmission simulations also support the notion that if sounds are generated at both (left and right) phonic lips at the same (or nearly the same) time, they could converge into a beam with higher amplitude than might be produced by either source independently due to constructive interference. This is the kind of information that has never been verified for other odontocetes, even though a few workers have suspected that this is the case. When we move to simulations of other odontocetes we will be able to test whether it holds true and suggests a concept that is broadly applicable.

The gular pathway for sound propagation in odontocetes creates a new vision and significant implications for our understanding of hearing and a means for evaluating the potential impacts of high-intensity sound. It is clear from these results that the acoustic structure and function of the odontocete head deserve considerable additional research.

Finally, the results reported here must be considered with a healthy dose of skepticism because the simulations push beyond our current knowledge base for this species. At the same time, we have provided examples suggesting that the FEM-based method produces results that are reasonable and may substantially improved our understanding of odontocete bioacoustics.

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