

# ON NOVEL RECEPTION MODELS FOR BOTTLENOSE DOLPHIN ECHOLOCATION

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## 1. ABSTRACT

*Bottlenose dolphin (*Tursiops truncatus*) echolocation resolution greatly exceeds measured beampattern and conventional hearing model performance. We re-examine the idea that teeth might aid conventional hearing. Nerve conduction requires neural delay lines, a requisite that might be met by unexplained specialised cell arrangements already reported. Jawbone resonance displays selectivity at 25-35 degrees to one side of the rostrum that suggests the use of ambient noise or a passive sonar mode associated with head scanning.*

**KEY WORDS:** dolphin; echolocation; teeth; tursiops; sonar; hearing

## 2. INTRODUCTION – WHAT IS THE PROBLEM?

Dolphins have clearly evolved excellent echolocation capabilities but many aspects of how their biosonar works are still not fully understood. The echolocation system performance depends on three main areas of functionality; the transmit characteristics, the reception characteristics and the central nervous system processing. The major factors that constrain the spatial resolution of objects in three-dimensions are the transmit beamwidth, the receive beamwidth and the time resolution, the latter of which determines range resolution. The beam-width of both receive and transmit patterns are in turn constrained by fundamental physics. A very narrow linear acoustic beam simply cannot be achieved from a small aperture (defined in wavelength terms), either in transmit or receive modes.

### 2.1 Transmit characteristics

The transmit beampatterns of the common dolphin (*Tursiops truncatus*) have been extensively measured (c.f. [1]). The typical beamwidths both horizontally and vertically are on the order of 10 degrees. The type of echolocation click that is produced can vary considerably, but studies have shown that *Tursiops truncatus* typically uses short broadband pulses or clicks that have durations between 50 and 200 microseconds [1]. Although often centred around 110 kHz, the frequency content can be as high as 170 kHz at the -10 dB point referenced to the peak spectral value. Figure 1 shows two typical clicks recorded by one of the authors from a single *Tursiops truncatus* called Elele during her examination of a highly spatially-structured object placed behind a visually opaque screen. The clicks have centre frequencies of 140 and 150 kHz, with upper -10dB frequency limits of 160 and 170 kHz respectively. The click durations are very short, 35-45 microseconds. These data were recorded while Elele was performing a very high-resolution target recognition task, and perhaps this goes some way to explaining the high frequencies present in her echolocation clicks. For a given spatial aperture, higher frequencies generally permit higher angular resolution, both in transmit and receive modes.

## 2.2 Receive characteristics

Norris [2] first suggested that the 'special' lipid overlying the pan bone, which extends to the tympanic bulla, plays a major role in channelling sounds to the bulla, which are otherwise acoustically isolated from the bones of the head. The importance of the lower jaw in sound reception during echolocation was demonstrated by Brill *et al.* [3] using a trained *Tursiops truncatus* performing a target discrimination task using acoustically opaque and acoustically transparent neoprene 'hoods' covering the lower jaw. The current understanding is that conventional hearing relies on the fat channels of the lower jaw ducting sound into the middle ear.

Johnson [4] reports that a bottlenose dolphin can hear over a wide frequency range between 75 Hz and 150 kHz, and has good sensitivity (within 10 dB of the maximum) between approximately 15 kHz and 110 kHz. Above 150 kHz, the upper frequency limit of hearing cuts off very sharply, at about 495 dB per octave [5].

This raises a problem. We have already noted that Elele's clicks were centred on 140-150 kHz and had significant energy up to 160-170 kHz. The use of high frequency content in the clicks is consistent with requiring high spatial resolution, but only if the scattered echo can be sensed.

Hearing reception beamwidths are broadly similar to transmit beamwidths, about 10 degrees wide at the  $-3$  dB points w.r.t. the peak sensitivity in both vertical and horizontal planes at 120 kHz [1]. This is approximately equivalent in performance to a non-shaded circular aperture of some 75 mm, a scale comparable to the separation between the inner ears and hence consistent with physiological expectations.

Yet, Renaud and Popper [6] measured a minimum audible angle of 0.7 degrees in the vertical plane and 0.9 degrees in the horizontal plane for *Tursiops* with a broadband click signal of peak frequency 64 kHz, a far superior performance than suggested by the raw receive beamwidths despite operating at nearly half the frequency. This presents another problem; how is the dolphin able to attain such a high degree of angular resolution from a comparatively poorly-resolving conventional hearing beamwidth?

## 2.3 Higher nervous system processing

This is perhaps the least understood component of dolphin echolocation. The conventional model of hearing is that the inner ear of the dolphin acts somewhat like a bank of constant-Q filters, providing spectral intensity without phase information [7,8]. This is based on a morphological appreciation of the resonant properties of the basilar membrane in the inner ear and means that it would be impossible to perform phase-coherent processing. This disqualifies one candidate for the observed high degree of spatial resolution: matched filter processing of backscattered clicks. However, we do not know, for example, whether dolphins are able to perceive time separation

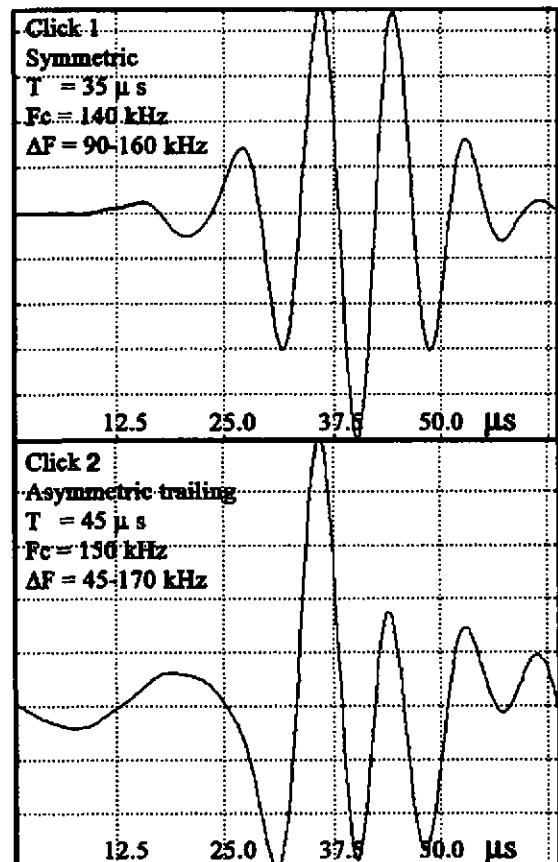


Figure 1. Two example echolocation clicks

pitch as suggested by Johnson *et al.* [9], which allows spectral resolution to be used to determine very small time delays between identical time-delayed copies of a broadband signal. Temporal discrimination between two signals has been measured at 50 microseconds [9], equating to a range discrimination of approximately 75 mm.

However, the problems of explaining the high degree of lateral spatial resolving ability and significant energy content at frequencies above the conventional hearing range of *Tursiops truncatus* remain.

### 3. IS DENTAL RECEPTION A PLAUSIBLE SOLUTION?

#### 3.1 The dental array idea

The lower jaw construct consists of two mandibular bones (fused into one mandible), two fat channels, and the teeth, all of which need to be considered as potential elements in the overall sound reception and conduction mechanisms. McCormick *et al.* [10], measured large electrical potentials generated in the organ of Corti in the cochlea when a vibrator was held against one of the front teeth of the lower jaw, indicating a strong innervated pathway for sound to interact with teeth and be perceived as sound. Goodson and Klinowska [11] examined the lower jaw as an acoustic construct using the tooth spacing and jaw geometry to compare various detection enhancement hypotheses, one of which implicated the tooth/mandibular nerve structure as part of a high frequency echo pulse receptor. They suggested that discriminatory sensing of a target echo, particularly during the final hunting phase leading to food capture, might exploit a dedicated high frequency receptor operating in parallel with the conventional wide band auditory sense organ. Dobbins [12] used their assumption that the nerve conduction speed would allow the teeth to act as pressure transducers such that an echo arriving from a direction along the axis of the row of teeth (end-fire) would result in the signals from all the teeth arriving at the central nervous system simultaneously so that they add together constructively. In this paper we examine the tooth reception model and extend it to consider the implications of realistic nerve and bone transduction speeds and the requirement for a delay-line mechanism in the CNS signal processing.

Odontocetes are homodonts which means that all teeth, within any one species, have the same morphology [13]. *Tursiops truncatus* has approximately 98 small conical teeth [14], evenly spaced with quite remarkable precision along the length of the jaw bones, that are commonly believed to have evolved for grasping and holding fast-moving prey such as fish or squid. It seems strange that *Tursiops truncatus* does not also have some flat teeth for grinding, as other predators do, to make digestion easier. There appears to be some cost to being a predatory homodont, and this suggests there must be some compensatory benefit.

#### 3.2 The dental pattern of a specific subject

The average tooth spacing for 3 adult *Tursiops* was reported by Goodson and Klinowska [11] to be 11.4 mm. For Elele, the young *Tursiops truncatus* we consider, the average tooth spacing has been estimated from the photograph shown in Fig. 2 to be 9.4 mm. Goodson and Klinowska [11] noted an offset equivalent to one half an inter-tooth spacing between the left and right dental lines in each jaw. They considered this significant in the performance of the teeth as an acoustic receiving array. From the

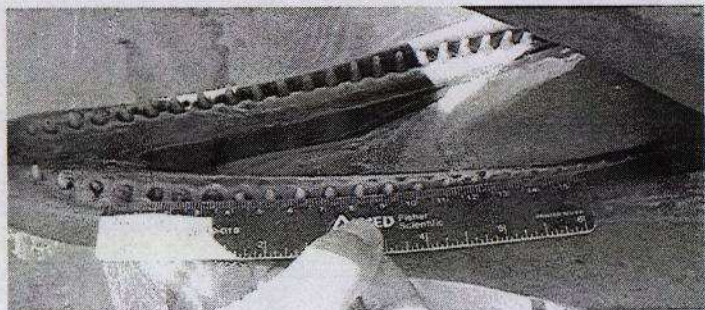


Figure 2. Elele's dental arrangement.

photograph in Fig. 2 we do not see a clear offset in Elele's tooth pattern. We have chosen to consider all the teeth embedded in both jaws as a single array. We consider the reception characteristics of both lower and upper jaws together, the teeth of which must be offset by approximately one-half an inter-tooth spacing in order not to clash. This effectively results in the same set of teeth positions in the horizontal plane of the jaws as Goodson and Klinowska [11] would use, simply distributed differently between upper and lower instead of left and right sides of the jaws. We have therefore modelled Elele's dentures as being axi-symmetric in this plane.

Rather than model each jaw as a pair of linear arrays with constant angular separation, the horizontal spatial distribution has been modelled as a parabolic curve. A tangential line drawn through the midsection has a linear angle of 10 degrees, a little more than the 6 degrees used by Goodson and Klinowska [11]. The final tooth pattern is shown in Figure 3, where circles represent teeth in the lower jaw and crosses represent teeth in the upper jaw.

### 3.3 The teeth as an innervated array

In Odontocetes, the trigeminal nerve that serves the teeth is second in size only to the vestibulocochlear nerve [for review, see 15]. Axon diameter and overall nerve size is correlated with nerve speed and presumably physiological importance. This may reflect the high tactile sensitivity of the skin, tongue or teeth since the size of a nerve generally indicates the number of individual neurons it contains or the diameter of those neurons [16]. These factors, along with myelination of the nerve, serve to increase nerve conduction speed [17], a feature we shall address later. For the moment, we suppose only that high-frequency acoustic waves, potentially those best able to assist in high-resolution discrimination tasks but perhaps above the best hearing range of a *Tursiops truncatus*, interact with the teeth and that this generates a signal that is conducted to the central nervous system (CNS). The most likely mechanism for tooth response is probably that proposed by Goodson and Klinowska [11], tooth resonance. This could be a process with a relatively high Q, producing a long resonant oscillation in the tooth of narrow bandwidth. A CW beamformer is then the appropriate choice to investigate the resulting sensitivity of this model of a dental array.

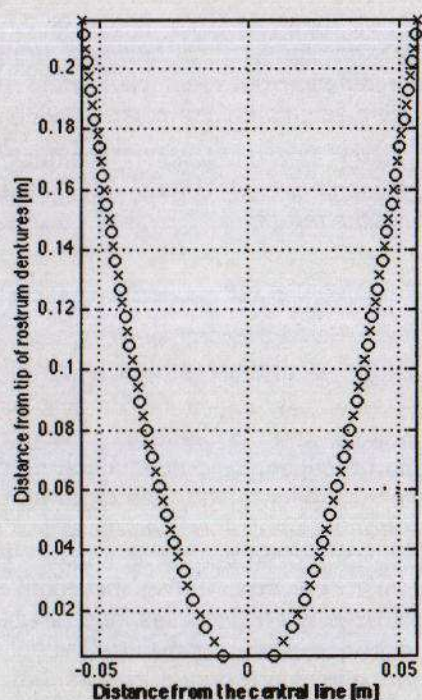


Figure 3. Modelled dental pattern

#### 4. IDEALISED BEAMFORMING

If we consider the beamforming potential of the modelled tooth array as if each resonant tooth output were available to a beamforming system, we can calculate the sensitivity of such an array in dB with respect to the signal level from only one tooth as a function of incident angle and frequency. The result is the sensitivity pattern shown in Figure 4, which shows the sensitivity of the dental array to continuous wave (CW) frequencies between 100-170 kHz at angles from 0 (directly in front of the rostrum) to 30 degrees to one side. The sensitivity is symmetrical, so positive and negative angles would give the same result. The most obvious and surprising feature is the very highly selective sensitivity on axis at 160 kHz, providing signal levels 39 dB above that of a single tooth. This represents a coherent sum of over 90% efficiency over the 92 teeth in the model. The main lobe at 160 kHz has a double-sided width of less than 4 degrees at the -3 dB points, considerably narrower than the conventional hearing receive beam and more in line with observed angular resolution.

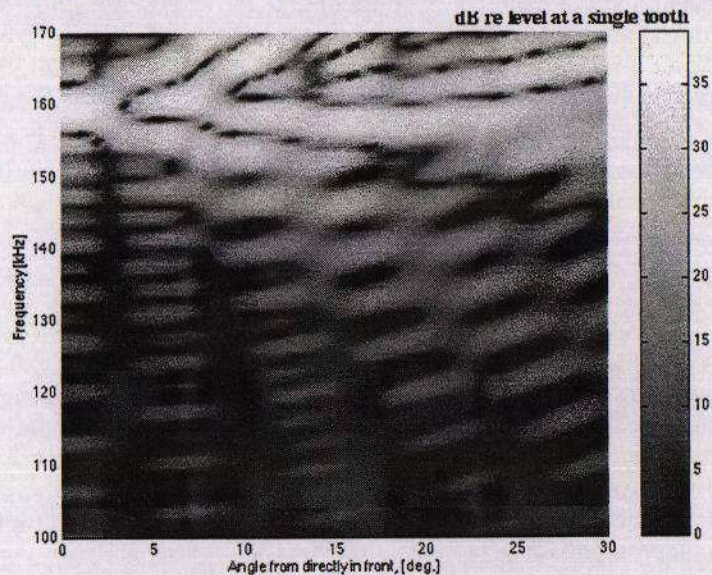


Figure 4. Frequency-angle sensitivity plot for the idealised zero-lag modelled dental array

An on-axis insonifying pulse will take approximately 140 micro-seconds to travel from the foremost tooth in the rostrum to the rearmost tooth (via seawater and similar acoustic impedance materials). The length of the insonifying pulse may only be 35 - 45 microseconds. If each tooth resonates for less than 125 microseconds or so, the foremost teeth will no longer be resonating by the time the acoustic pulse reaches the rearmost teeth, preventing a coherent summing of the signal. To obtain a resonant duration of 125 microseconds requires a Q of about 20, corresponding to a frequency selectivity of about 8 kHz at 160 kHz centre frequency. This bandwidth is consistent with the width of the lobe observed in Figure 4.

The obvious difficulty with this idealised beamforming is that the differential lengths of the nerves have not been taken into account, and these will add significant delays to the coherent summed signals. We address this issue next.

#### 5. BEAMFORMING WITH REALISTIC NERVE CONDUCTION SPEEDS

The smaller sensory nerve fibres within human teeth and in the mandibular nerve have reported conduction speeds of 1 - 40 m/s [18]. In the case of the tooth pulp, conduction velocities would be a maximum of about 40 m/s (A-delta and C fibres), and in the proprioceptive nerve fibres (A-alpha type) the conduction velocity is between 80 to 100 m/s. This is similar to speeds observed in intra-dental nerves of cats, 30 - 45 m/s [19]. The fastest nerve conduction speed in myelinated nerves, 120 m/s, is still slow compared to the ~1500 m/s speed of sound in seawater. Goodson and Klinowska [11] noted that the slow propagation of nerve impulses implies that a delayed response related to the tooth position in the jaw must exist, and, since the tooth nerves proceed in parallel as part of the mandibular and then trigeminal nerve, that the signal arrival times at the pons, for

onward processing in the higher brain centres, are dependent on the individual nerve lengths. They proceeded to assume that the various lengths of these nerve delay lines would translate the responses received from the teeth along one side of the jaw as they are sequentially insonified by an on-axis sound pressure wave into a single time coincident event.

We have taken a nerve speed of 100 m/s as representative of the fastest likely speed for the dental nerves. By calculating the cumulative distance between teeth along the jawline we have estimated the delay for each tooth and introduced this into the beamforming algorithm. The result, for the same range of frequencies and angles as in Fig. 4, is shown in Fig. 5. It is very clear that, although the maximum sensitivity can be almost as high as the idealised beamformed signal in Figure 4, there are no stable coherent lobes and that such a system could not be useful.

How, then, could the nerve delay problem be solved? The only candidate seems to be if there were a plausible delay-line system in the CNS that could introduce variable delays of the order of 2 milliseconds, such that the nerve-induced delays could be evened out to restore the desirable highly-selective sensitivity lobe in Fig. 4.

Zook *et al.* [20] described some unusually ordered cell arrangements within three auditory brainstem cell groups: the ventral cochlear nucleus (VCN), the medial nucleus of the trapezoid body (MNTB), and the ventral nucleus of the lateral lemniscus, where part of each cell group is distinguished by an orderly alignment of cells into straight rows or columns. They went on to estimate the range of delays possible in the dolphin brainstem [21] and proposed that the VCN and MNTB cell arrangements might be two components of a larger functional network in an auditory circuit. The problem with their explanation was that the measured delays were in the range of 0.21 – 1.7 milliseconds. For phase coherent auditory processing, this would corresponded to discriminating amplitude modulations in the range 290 Hz to 2.4 kHz, which is inappropriate for echolocation, being far too low.

So, delay line mechanisms in the auditory cortex have already been found, and their function remained a puzzle since the estimated delays seemed ill-fitted to echolocation frequencies detected and processed by conventional hearing mechanisms. Yet here we have found a need for a set of delay lines with almost exactly the lengths discovered, to correctly phase dental nerve signals. Might it be possible that this is the function of these delay cells and that a selective high-frequency sense derived from tooth response might assist conventional hearing in high-resolution echolocation tasks?

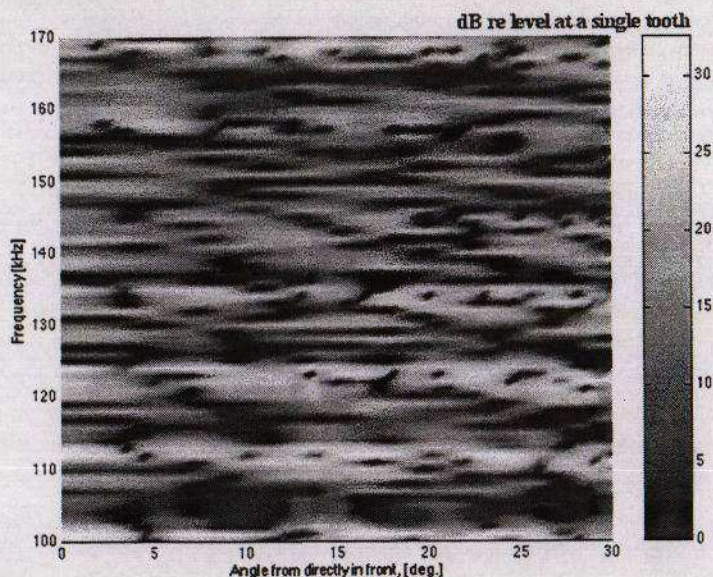


Figure 5. Frequency-angle sensitivity plot for the nerve speed-lagged modelled dental array

## 6. BONE CONDUCTION POSSIBILITIES

The teeth might also play a role in sound reception by bone rather than nerve conduction. A gomphosis is a fibrous, mobile peg-and-socket joint. The roots of the teeth fit into their sockets in the mandible and maxilla and are the only known examples of this type of joint. Bundles of

collagen fibres pass from the wall of the socket to the root; they are part of the circumdental, or periodontal, membrane. There is just enough space between the root and its socket to permit the root to be pressed a little further into the socket during biting or chewing, thus transmitting a sense of proprioception (or movement) via the trigeminal nerve to the central nervous system (CNS). These tight joints would allow sound picked up by teeth to be transmitted deep into the bone. In contrast to nerve conduction, bone conduction speeds are fast. The speed of sound conduction in human bone has been reported to be 3300 m/s [22]. The speed of sound in heel bone (calcaneum) lies between 1900 - 1550 m/s for young subjects and osteoporotic patients respectively [23]. It seems reasonable that for the purpose of this argument, we could assume bone speeds in the range of 1900-3300 m/s for dolphins. In this scenario, the entire jawbone would need to be driven as a whole in response to the driving forces at the individual teeth. Using the slower speed in this range, 1900 m/s, produces an intriguing beampattern, shown in Fig. 6. There is little coherent sensitivity at higher bone speeds or at most angles, but for a bone speed of 1900 m/s there is a strong coherent sensitivity over a broad frequency range at about 25-35 degrees.

In contrast to the highly-frequency-selective tooth resonance mechanism, this sensitivity is broadband and therefore suitable for retaining the character of broadband pulses without resonance.

To test this idea, the beam simulation code was modified to model the pulse train resulting from summed echolocation clicks, using a typical click as input. The

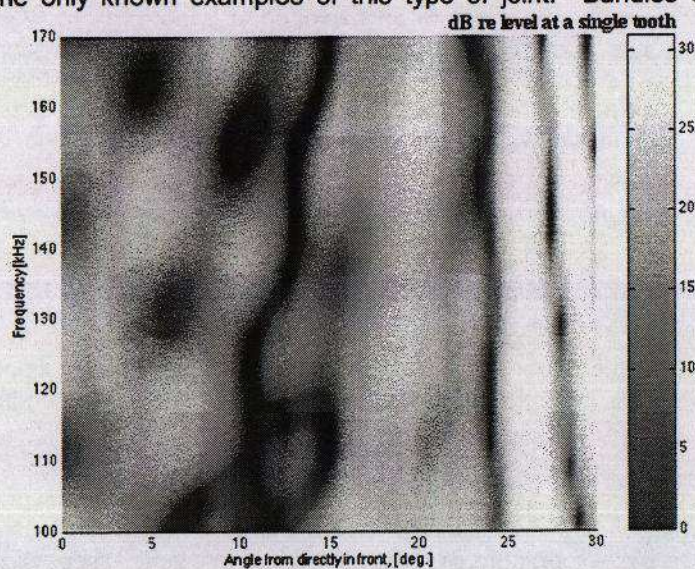


Figure 6. Frequency-angle sensitivity plot for the bone speed-lagged modelled dental array

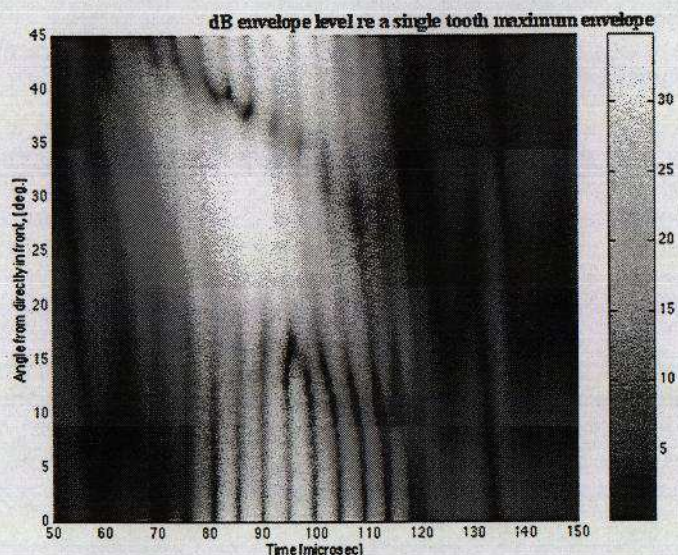


Figure 7. dB plot of the summed pulse envelope re the maximum envelope from a single tooth for bone conduction.

result is shown in Fig. 7. Unlike the earlier figures, Fig. 7 shows the sensitivity as a function of the time series and angle. A Hilbert transform has been used to estimate the pulse envelope, normalised to the single tooth envelope maximum, before taking the logarithm to give dB values. The compact pulse is clearly seen at about 25-35 degrees off the rostrum axis, arriving at about 80-90 microseconds after the pulse reaches the first tooth at the rostrum tip.

If this sensitivity were to be exploited, it is not clear how. Little click energy radiates out of the melon at such a high angle, even less at the higher frequencies. For short echolocation ranges, *Tursiops truncatus* would be unable to sweep its head fast enough to transmit a click, then rotate 30 degrees to receive the backscattered echo. At 50 m target range, this movement would require a maximum rostrum speed of about 2.5 m/s.

Finally, the angular resolution is rather poor compared to the other mechanisms we have considered.

Nevertheless, dolphins are observed to scan their heads back and forth during exploratory activity, and perhaps this is linked to this peculiar sensitivity at 25-35 degrees off the rostrum axis.

The most striking feature is the broadband coherence of this lobe, indicating, perhaps, that it could be useful for receiving broadband signals or signals of opportunity of unknown a-priori frequency content. If dolphins were able to exploit ambient noise and sources of opportunity, this could be a mechanism to aid their conventional hearing.

## 7. CONCLUSIONS

We believe that the dental and jaw mechanisms discussed in this paper may serve to assist the conventional hearing mechanisms in at least two distinct ways. The innervated resonant-tooth model provides a highly frequency-selective sensitivity on the rostrum axis, provided that delay lines are associated with the processing. Delay lines have indeed been observed in the auditory cortex of the correct magnitude to perform this task, and of incorrect duration to be useful in echolocation processing by conventional hearing. This may be part of the puzzle of how *Tursiops* achieves reported echolocation performance. In addition, bone conduction could be significant in a non-resonating tooth model where a broadband response is useful. The only significant sensitivity lobe observed in this model was for bone conduction speeds near 1900 m/s, towards the lower end of the plausible range, where pulses were coherently summed at some 25-35 degrees to the side of the rostrum axis. This could conceivably be useful in exploiting broadband sources of opportunity, associated with head-scanning.

It seems we should consider a more holistic view of auditory perception that encompasses a greater diversity of mechanisms operating in parallel. Feng *et al.* [24] have reviewed behavioural and physiological data relevant to hearing in complex auditory environments. They report that behavioural data suggest that animals use spatial hearing and integrate information in spectral and temporal domains to determine sound source identity. On the physiological side, although little is known of where and how auditory objects are created in the brain, studies show that neurons extract behaviourally important features in parallel hierarchically arranged pathways. At the highest levels in the pathway these features are often represented in the form of neural maps. Further, it is now recognised that descending auditory pathways can modulate information processing in the ascending pathway, leading to improvements in signal detectability and response selectivity, perhaps even mediating attention. These issues and their relevance to hearing in real-world conditions must be considered with respect to any model systems for which both behavioural and physiological data are available.



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