

Biosonar sources in odontocetes: considering structure and function

In a recent paper in *The Journal of Experimental Biology*, Madsen and his colleagues, 'hypothesize that all toothed whale species only click with one set of their phonic lips at a time, and preferably their right pair' [(Madsen et al., 2010) see p. 3110 of their article]. This conclusion was based on a limited data set from one odontocete species, and runs counter to established literature that may not have been adequately reviewed.

The authors of the paper in question:

- (i) offer a presumptuous hypothesis [proposing to know how all (73) odontocete species behave from their observational data for one species];
- (ii) demonstrate overextended extrapolation (claiming knowledge of behavior for which they have no data);
- (iii) provide an inadequate description of methodology (with no means to determine whether they actually studied echolocation);
- (iv) present a functional proposal that does not match the morphological complexity in the sound generation apparatus;
- (v) fail to adequately consider contradictory anatomic evidence;
- (vi) omit contradictory reports in long-established literature.

In my view, it is somewhat presumptuous of these authors to posit the behavior of 70 or so species of mammals (the entire Suborder: Odontoceti) with any specificity, particularly when it is based on a single set of experimental observations using one small odontocete species.

Madsen and colleagues assert that the nasal apparatus on the left side can also be used to make clicks. But as their study never recorded a click from the left side, it is unclear how they could arrive at this conclusion. They then assert that the click generator on the left side is only used for communication, a function for which they also report no observations.

The methodological description by Madsen and his colleagues is inadequate to establish that they were, in fact, studying echolocation behavior. What exactly was the 'echolocation' task? For example, what was the size of the target and how far in front of the animal was the target placed? Was the fish only the reward, or was it also the target? How was the target presented? In any psychoacoustic experiment of echolocation behavior, safeguards must be in place to ensure that the animals are not using vision and are actually engaged in echolocation. There is no indication that the animals in Madsen and colleagues' experiments were blindfolded or otherwise prevented from solving the problem visually. Without these safeguards, they cannot claim to have studied echolocation.

There is also no indication of the level of difficulty of the task; was it target detection or discrimination? Madsen et al. report that their animals solved simple 'short-range echolocation'. As a consequence, it is possible that they posed a problem so trivial that it did not require extraordinary skill or effort for the animals to solve.

Another primary objection is that their assessment of function does not match the anatomic complexity in the odontocete forehead. It would seem that the anatomic complexity of pertinent bilateral sound generation features (phonic lips and associated structures) is being maintained by natural selection, and this argues for functional complexity.

Anatomic structures tend to atrophy from disuse. Therefore, it is reasonable to expect that disuse of a biological structure would lead to inheritance of 'architectural flaws' that would accumulate over time if natural selection were not exerting pressure to keep the structural arrangement within some narrow range of tolerance. But despite their argument for disuse (see p. 3110 of their article), using sperm whale anatomy as a foil, Madsen and colleagues propose that the opposite is true in porpoises – that the structural complexity of

both sets of phonic lips is conserved. It would appear that Madsen et al. have the worst case scenario to prove their case, because both sets of phonic lips and associated tissues in porpoises are intricate and virtually symmetrical (Cranford et al., 1996). The intricate bilateral sound production apparatus in the Odontoceti is nearly ubiquitous and therefore problematic for Madsen and colleagues' all-inclusive conclusion.

This conundrum is acknowledged in the last sentence of their paper: 'Why they seemingly carry two identical phonic lip pairs while apparently only using one pair at a time for clicking needs to be addressed in future experiments...'

This statement reveals a weakness in their central conclusion. They are aware of the contradiction but may not have considered its implications or alternative explanations. Rather than address this contradiction directly, they suggest it is a prompt for additional research. No such catalyst is necessary; investigations of odontocete sonar signal generation have been a source of vigorous debate in cetology for almost half a century (Cranford and Amundin, 2003).

Madsen and colleagues have also omitted pertinent literature, including several studies that appear to contradict their primary conclusion: that all odontocetes click with only one set of lips at a time – preferably the right pair.

In 1962, John Lilly worked with bottlenose dolphins and reported, 'Our animals tend to click only on the left side and whistle only on the right side and can do so simultaneously or separately' [(Lilly, 1962) see p. 522 and fig. 8 of his paper]. Madsen and colleagues apparently also did not consider the results reported by Dr Lilly in 1978 (Lilly, 1978). Lilly described an experiment whose design is similar to that used by Madsen and colleagues. Lilly [(Lilly, 1978) see p. 68 and fig. 7] described dual (stereo) click sources (one on each side of the head). These studies directly contradict Madsen and colleagues' conclusion that all odontocetes preferably use the right side for clicking.

In addition, Madsen et al. did not cite the seminal work (in multiple papers) conducted by Dr William E. Evans, which can be directly compared on the issue of odontocete sonar signal generation. In 1973, Evans recorded, 'click formation on either or both sides of the blowhole' (Evans, 1973). Like Madsen and colleagues, Evans also used contact hydrophones and hydrophone arrays to record pulses emanating from the head of bottlenose dolphins (*Tursiops truncatus*). In calculations that must be similar to those of Madsen et al., Evans reported two distinct pulses being produced by two sources, one on each side of the midline [(Evans, 1973) see p. 197, paragraphs 1 and 2 of his paper], and that their dolphins could use 'either or both'. This work also contradicts Madsen's conclusion because Evans indicates that dolphins can produce sonar clicks from both sources, separately or simultaneously.

In some respects, if Madsen et al. agree that all odontocetes (except sperm whales) have two click sources then there is only disagreement about function. The evidence that bilateral sources are being maintained by natural selection suggests that these sound generators are used when needed and probably for a multiplicity of functions. Contrary to the suggestion of Madsen and colleagues, it is unlikely that it can be known how the broad spectrum of odontocete species will behave from the paucity of evidence that now exists. The arguments put forth by Madsen and colleagues are in doubt because of deficiencies in the methodological description and contradictory evidence in the established scientific literature.

References

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Response to 'Biosonar sources in odontocetes: considering structure and function'

If we knew how all 73 species produce sound, it would be a conclusion and not a hypothesis: a hypothesis is a fundamental part of experimental biology where a general mechanism is proposed from a limited data set at hand, and then subsequently tested through falsification attempts in future experiments. Cranford seems to use the terms 'hypothesis' and 'conclusion' interchangeably, as he later writes: 'Madsen ... omitted ... studies that appear to contradict their primary conclusion: that all odontocetes click with only one set of lips at a time – preferably the right pair'. That is our hypothesis, not the conclusion. Additionally, Cranford incorrectly states that we base our hypothesis on a single species and that we ignore pertinent literature. In our paper, we carefully cite six anatomical and modelling papers, all reporting that toothed whales primarily click with their right pair of phonic lips, and here we also point to recent studies by Au and colleagues (Au et al., 2010) and Dubrovskiy and Giro (Dubrovskiy and Giro, 2004) showing the same. Our hypothesis is thus not based on a single species/study.

As missed references in which the findings are purported to be inconsistent with our hypothesis, Cranford points to Evans (Evans, 1973) and Lilly (Lilly, 1962; Lilly, 1978). He states that Evans recorded 'click formation on either or both sides of the blowhole'. Here Cranford selects a few words, which in isolation convey a message that is at odds with the text from which they were extracted: 'More recent work ... provides convincing evidence that the nasal plugs may well be involved in the production of whistles as well as clicks, the whistles being produced on the left side and the clicks on the right side. This does, however, not account for the omnidirectional characteristics of the whistles and the variable directivity pattern of the echoranging clicks which seems to favour click formation on either or both sides of the blow hole'. Here Evans introduces the speculation, re-proposed by Cranford and colleagues (Cranford et al., 1996), that dynamic beam formation may be achieved by simultaneous activation on both sides, but Evans absolutely never recorded what Cranford quotes him for.

The studies by Lilly (Lilly, 1962; Lilly, 1978) do claim clicking on both sides. Cranford quotes Lilly (Lilly, 1962) this way: 'our animals tend to click only on the left side and whistle only on the right side and can do so simultaneously or separately'. The correct quote reads: 'One of our animals tends ...'. Again Cranford applies his unique quotation technique in omitting the first two words and the 's' to convey that all the animals did this. While Cranford's rendition of the text could cast doubt on the general validity of our hypothesis of predominant right-side bias, the correct quote does not falsify our hypothesis.

Also, Lilly's studies suffer from poorly documented methodology, which contrasts with the certainty with which his bold and speculative conclusions are presented. He states, for example, that high frequency clicks are generated from bursting slime bubbles in the larynx and are radiated *via* resonances of the dolphins' teeth to form a 3 deg beam – claims that have all been falsified since. The data in Lilly [(Lilly, 1978) see his fig. 7] do not demonstrate simultaneous click production: the

two hydrophones will pick up the same click, no matter whether it is the result of one or two sources. Hence, in our view, no experimental data demonstrate that the two pairs of phonic lips produce two pulses to form a single click.

On the basis that we did not conclusively demonstrate active echolocation, Cranford questions the validity of our clear-cut results. However, we fail to see how this falsifies the single source hypothesis. Does this mean, for example, that studies on bird vocal production must be discounted if the experimenters fail to prove that the bird was actually communicating while vocalizing in the laboratory? On p. 3109 in our paper (Madsen et al., 2010) we do state that we cannot exclude the possibility that behavioural settings might exist in which the animals produced clicks with the left or both pairs of phonic lips. But why? If something is particularly easy to read, would you then close one eye, because it would be overkill to read it using both? Many animals use one of two bilaterally symmetric body parts more than the other. Could it be that toothed whales are simply 'right handed' in their click production?

Cranford argues that toothed whales with two pairs of phonic lips must use both, as otherwise the inactive one would degenerate. Actually, most toothed whales do have a hypertrophied right pair of phonic lips (Cranford et al., 1996), which makes porpoises, not dolphins, the obvious choice for testing Cranford's hypothesis that both phonic lips pairs are actuated simultaneously to produce a single click. No data have shown that to occur and, as outlined in our paper, the advantages are small and in some cases mutually exclusive. Given that simultaneous actuation of the phonic lip pairs would require sub-microsecond motor-neuronal timing, such a system, if at all possible, would have to be the result of a heavy selection pressure to provide real survival value. But double pulses, unless the animal had perfect timing from the evolutionary onset, would pose problems: imperfectly controlled they would create beams either pointing in random directions or with dips in the spectra at random frequencies, rendering the echoes unfit for classification of targets. Double pulses with delays longer than the ear's integration window would impede the sonar function by creating range ambiguities. So unless toothed whale ancestors got it exactly right the first time, it would impede an already functioning system. Such complexity is hard to reconcile with the principle of parsimony. Thus, from our results, the peer-reviewed literature, the severe functional problems of simultaneous actuation of two sources and the limited advantages of doing so, we maintain that the simultaneous click production hypothesis is as dead as the animals on which Cranford based it.

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