

# Neurophysiological Findings Relevant to Echolocation in Marine Animals

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**M**ANY MARINE ANIMALS produce sounds either as vocalizations or otherwise. Theoretically any of these may be capable of providing the basis for echolocation. Even sounds produced from sources completely independent of the animal may be used, as is believed to be true for some blind persons (refs. 1 to 3) and in monaural localization of sound sources in normal people. Whether a given species employs echolocation or in what degree of refinement it employs echolocation cannot be decided from the quality of the sounds available in its environment or from the properties of vocalizations it may produce. Direct behavioral experiment is essential, manipulating the emitted sounds, the echos or the auditory receiving system.

Among marine animals, only porpoises have been convincingly shown to utilize echolocation (ref. 4). Sperm whales and other toothed whales are presumed to use fine grained sonar since they are closely related to porpoises and since they produce click-like sounds resembling the echolocating click of porpoises (ref. 5).

Baleen whales on the other hand are believed not to use a high resolution sonar since they lack such sounds both in respect to the click-like form and the ultrasonic frequencies; they may well detect the bottom and the surface, icebergs and other large objects by echos from their low frequency vocalizations; at least such echos are available as can be appreciated from hydrophone recordings of their calls (refs. 6 to 9).

Pinnipedes, especially sea lions, have been claimed to use sonar (refs. 10 to 18), but most authors have questioned the adequacy of the evidence (refs. 19 to 24).

Penguins have been supposed to use sonar (ref. 25) on the basis of the speed with which they catch fish in the dark! But in the absence of experiments on ear plugging or otherwise interfering with the postulated system the evidence does not yet justify the conclusion. Other swimming birds (loons, etc.) and mammals (otters, dugongs, manatees) are too little known for any significant statements. Although many aquatic reptiles, teleosts, and invertebrates make sounds, none has as yet

been really tested for the use of sonar in publications of which we are aware (ref. 26).

The neurobiologist using only physiological methods cannot say whether a species uses echolocation, either for fine grained object assessment or for simple ranging. He can however hope to discover specializations and differences between species potentially relevant to such accomplishments. He may be able to give clues to the important parameters or stimulus qualities which the nervous system is particularly equipped to discriminate. He may be able to distinguish those parts of the auditory system more likely to be concerned with echolocation than with other kinds of sound analysis, and he may be able to point to structures that act as sound paths, plot receptive angles, and the like.

The first physiological study that undertook these questions on a marine mammal was that of Bullock et al. (ref. 27) on central auditory mechanisms in a series of 29 porpoises, under anesthesia, recording the evoked potential in the midbrain to controlled sounds. McCormick et al. (ref. 28) recorded the cochlear potentials from the inner ear in porpoises. Bullock and Ridgway<sup>1</sup> have studied the evoked potentials in a series of nine unanesthetized, implanted porpoises, and Bullock et al.<sup>2</sup> have studied the evoked potentials in a similar series of sea lions.

#### COCHLEAR POTENTIALS FROM PORPOISES

McCormick et al. (ref. 28) recorded cochlear potentials from anesthetized dolphins. Up to 100 kHz the slope of the sensitivity curve was found to be similar to Johnson's be-

havioral curve, but cochlear potentials were recorded as high as 250 kHz. These potentials were used also to test and discard the idea that has persisted up to recent times that the external auditory meatus is a useful and significant route for sound to enter the ear.

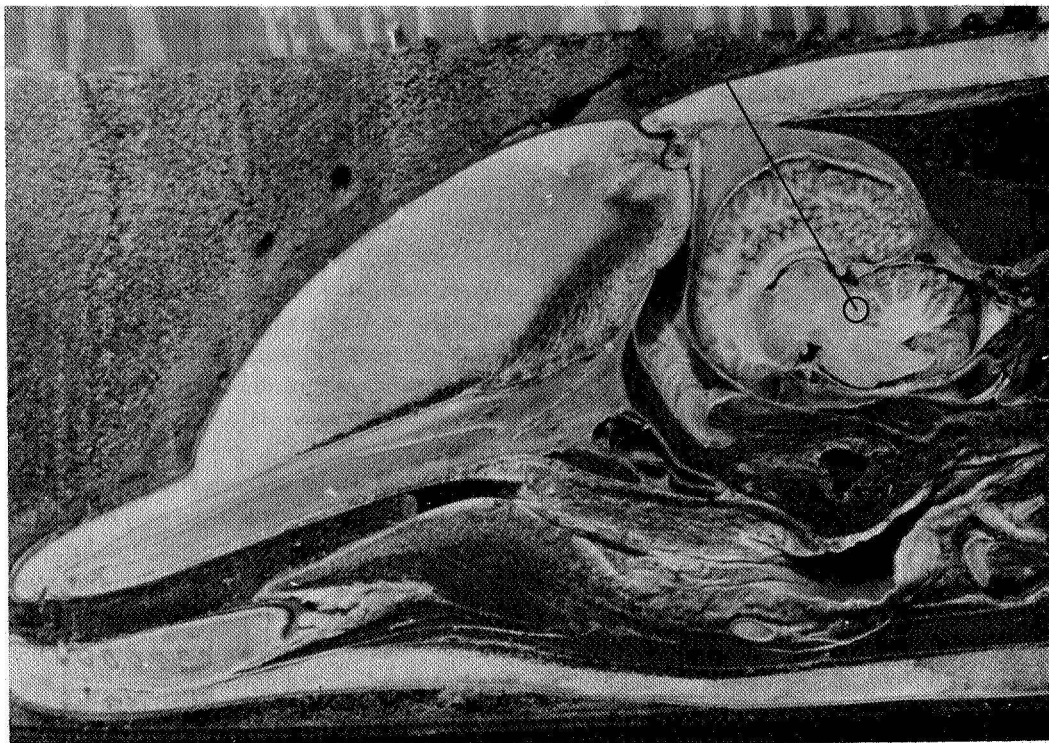
#### EVOKED POTENTIALS IN THE MIDBRAIN OF PORPOISES

Evoked potentials are shifts in the voltage between some point in the brain and a reference electrode elsewhere in the brain or outside of it, time-locked to and elicited by some stimulus under the control of the investigator. The term is generally used for compound potentials representing the activity of many cells as distinct from microelectrode recordings from single units. This is both the strength and the weakness of the evoked potential method. It gives a representative view of the response characteristics of a large sample of reactive units in some proportion to their prominence and synchrony. On the other hand it hides the heterogeneity of neuronal types and displays the algebraically summed field potential from an arbitrary fraction of the population—mixing excited and inhibited, sharply and broadly tuned, simple and complex units. When single units are difficult to get or the adequacy of representation of the whole population of units is in question, the evoked potential can unequivocally show that the central nervous system is sensitive to or discriminates certain stimulus parameters (refs. 29 to 32).

This method has been applied to porpoises using sharpened needle electrodes and fine wires (both however in the "macroelectrode" category)—a single probing electrode in the anesthetized series and arrays of seven to 18 electrodes along a supporting shaft implanted at operation into the brain in the series studied in the unanesthetized state (fig.

<sup>1</sup> BULLOCK, T. H.; AND RIDGWAY, S. H.

<sup>2</sup> BULLOCK, T. H.; RIDGWAY, S. H.; AND SUGA, N.: Acoustically Evoked Potentials in Midbrain Auditory Structures in Sea Lions (*Pinnipedia*). *Z. Vergl. Physiol.*, vol. 74, 1971, pp. 372-387.



**FIGURE 1.** Near sagittal section of the porpoise *Tursiops truncatus* showing path of the electrode array used in experiments recording from inferior colliculus. That structure is encircled and is about the size of the circle. Electrode array consists of axial shaft with either seven or 18 independent electrodes of fine wire, one exposed every few millimeters.

1). The electrodes are in each case inserted through small holes in the skull and traverse a good part of the brain in reaching their target, just as in a standard technique used on man and laboratory animals.

Our studies to date on cetaceans and pinnipeds have concentrated on recording in midbrain auditory centers. At higher levels, especially the cortical, the auditory areas are likely to be very extensive and to give more divergent results from experiment to experiment, unless the auditory areas are carefully mapped and landmarks established to permit using the map on each specimen. In addition, our evidence shows that higher levels are

more likely to be concerned with more complex auditory processing such as that involved in social communication. These levels certainly need to be studied in future investigations. Midbrain centers, especially the inferior colliculi, are intermediate level centers for analysis of auditory input. They may be specialized to extract information about special features of the stimulus (such as temporal relations, localization in space and the like) to judge from the physiological experience from cats and bats and from general vertebrate and cetacean anatomy (ref. 33 to 37). Although the inferior colliculus is not as spread out as the auditory cortex and the

evoked potentials are more nearly alike from experiment to experiment, it is enormously hypertrophied in the porpoise relative to non-auditory structures in the brain and is no doubt differentiated topographically in ways that remain to be determined in future studies. Our electrodes were sometimes in the nucleus of the lateral lemniscus, a closely related structure on the input side of the colliculus.

#### *Use of Evoked Potentials*

Under the conditions of these experiments the electrodes are sensitive to events in a mass of brain tissue at least a cubic millimeter or two in volume so that the properties described are those of a whole region but a quite local region. The form of the potential can be drastically altered by shifting the electrode 1 or 2 mm. An electrode 5 mm from the colliculus may not see any activity in response to sound stimuli even with a considerable amount of averaging of repeated responses.

The inferior colliculus is in the middle of the head and, even though large in cetaceans, is a difficult target to hit blindly with long electrodes inserted through small holes in the skull. This is routinely done with millimeter accuracy in cats and humans where there are prominent skull landmarks visible or palpable from the surface and where atlases and X-ray

monitoring are well developed. We used a stereotaxic device built especially for *Tursiops* in order to insert the electrodes into targets located on previous dissections. Due to common asymmetries of the skull and of external landmarks like the blow hole as well as to the difficulty of precise leveling of the head, we felt fortunate, after Dr. Ridgway had accumulated some experience, that he was able to place one or two of the electrodes on each penetration into an active area; that is, a location giving evoked potentials with a good signal to noise ratio in response to sound stimuli.

Figure 2 shows a representative form of midbrain evoked potentials in response to a 300/sec train of clicks. Note that the individual deflections in the evoked potential may be less than a millisecond wide indicating that, although compounded of many unit responses, there must be a high degree of synchronization in a certain population of cells. It also shows the high degree of consistency of the wave form to successive stimuli, giving confidence that details of the complex shape may be significant indicators of sensitivity to stimulus parameters.

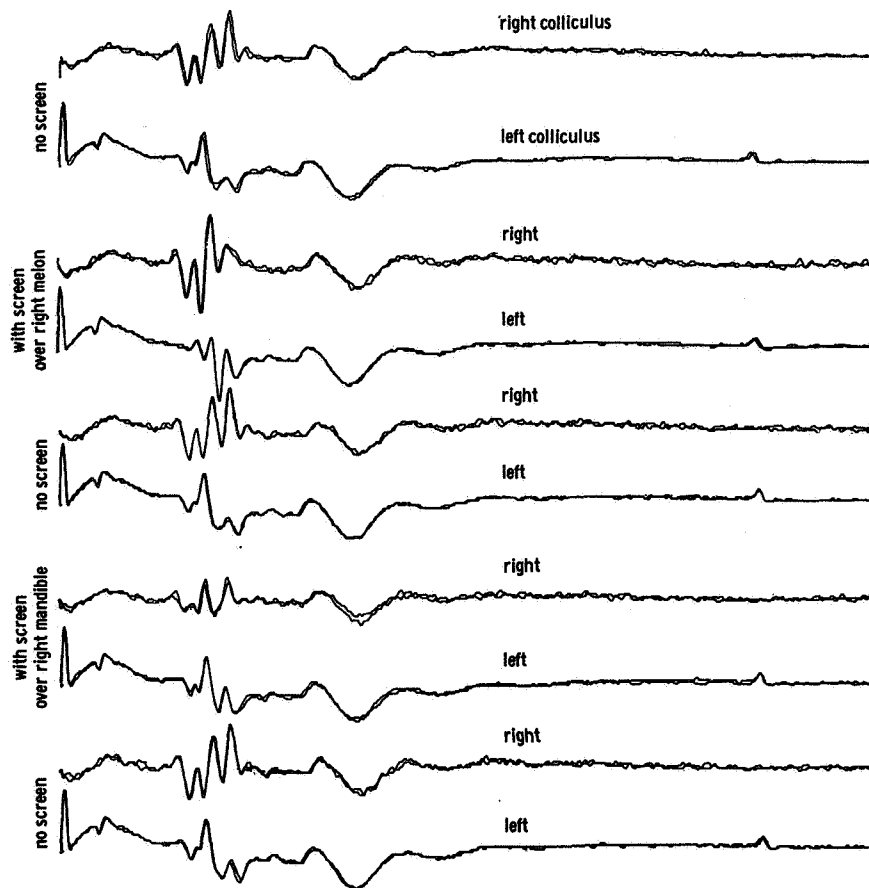
The sensitivity of this measure of brain response to subtle aspects of the stimulus is shown in figure 3. Slight alteration of the composition of the short tone burst delivered from a speaker as a result of interposing a thin slip of notepaper close to the surface of



**FIGURE 2.** Evoked potentials recorded in inferior colliculus during a train of tone bursts, each 0.3 msec in duration including 0.1-msec linear rise followed by 0.1-msec linear decay, composed of 90-kHz sound at  $-15$  dB referred to an arbitrary high intensity, repeated at 300/sec. Loudspeaker and porpoise's head were in the air 75 cm apart (2.2 msec sound conduction time). Sixty-four sweeps computer-averaged. Brief tone bursts every 3.3 msec evoke a potential after latency of 3.5 msec corrected for air time, consisting of a short complex of deflections less than 1 msec wide (ref. 27).



the animal drastically changed the shape of the evoked potential, especially on one side of the brain, even though not attenuating the amplitude of the response. This reversible and repeatable result is dependent upon the exact positioning of the slip of paper over a critical area of the porpoise's head. We do not know whether the alterations in wave



**FIGURE 3.** Sensitivity of evoked potential waveform to slight distortion of sound. Piece of thin notepaper  $10 \times 15$  cm was held 2 cm from the skin over portion of head indicated. Head and loudspeaker were in the air. Tone bursts of 50kHz, 0.5 msec in duration, and abrupt rise and fall repeated 20 times/sec were delivered by speaker on animal's right. Recording electrodes were in left and right inferior colliculi; deflection upwards represents positivity with respect to an indifferent electrode on the muscle. Slow components of the responses have been filtered out. Sixty-four sweep samples have been computer-averaged for each line; two successive averages are superimposed. Right and left recordings were made simultaneously under each condition. Time of full sweep equals 32 msec. Compared to the form of the evoked potential without the paper screen, the evoked potential on the left side in particular is drastically altered by placing the paper screen over the right melon, but without reduction in amplitude; with screen over the right mandible the form of potential in the right colliculus is most drastically altered. Paper screen position is critical to within a few centimeters (ref. 27).

form are due to recruitment of different populations of nerve cells or to changes in the discharge pattern of given units. It is nevertheless clear that this level in the brain is sensitive to small differences in sound quality.

This is one of the powers of the evoked potential technique since many types of units would not show this sensitivity and only the accumulation of a large sample of many different units would do so. The evoked potential wave form may well be far short of the behavioral discrimination power of the intact animal, but it can still reveal some surprising sensitivities as will be described and ones that are quite relevant to understanding behavioral achievement.

In the typical experiment on the porpoise inferior colliculus, the signal to noise ratio of evoked potentials has been large enough that many features can be distinguished on each individual response. However, for disclosing the differences in waveform to subtler differences in stimulus quality, a number of successive responses, which may be 8 or 16 or occasionally over 100 is averaged on a digital computer thus reducing the relative size of the non-stimulus-locked brain waves.

#### *Sound Path in the Porpoise*

The first result that might be mentioned using this technique is shown in figure 4. A small loudspeaker held close to the skin in air or in water or even in contact with the skin reveals that a sound can be more than 50 times weaker and still give a good response if the speaker is held close to the middle of the mandible (on the side opposite the electrode in the brain) than if it is held over the external auditory meatus. If the speaker is held some distance from the animal, it becomes apparent that there is a cone of sensitivity whose center projects from the mandible obliquely forward and down with the sensitivity

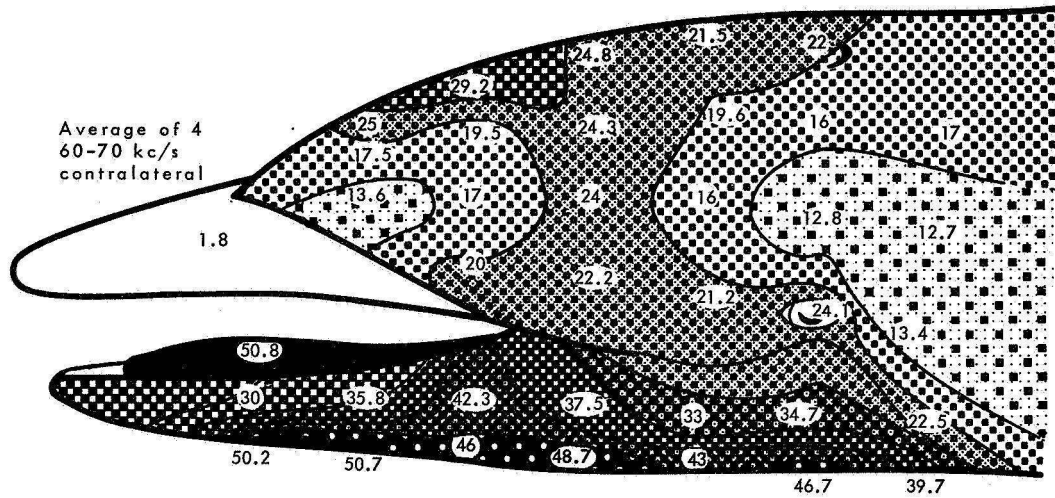
falling off steeply in all directions around this. From the side, from above, and from very slightly across the midline in front, sound must be much more intense in order to produce a response.

The maximum sensitivity over the mandible supports the speculation of Norris (refs. 38 and 39) of a fat filled canal through the mandible to the middle ear and argues against the proposition of Purves (refs. 40 and 41) and Fraser and Purves (refs. 42 and 43) that the external meatus is functional as a sound path (ref. 27). McCormick et al. (ref. 28) also argue against a functional meatus. Sound enters the head primarily through the skin far forward of the ear and mainly through the mandible, presumably to be conducted through some sound guide to the ossicles of the middle ear. In addition to the contralateral mandible, a second zone of somewhat lesser sensitivity is over the ipsilateral portion of the melon, the forehead-like structure over the upper jaw. Together with the somewhat beamed outgoing cone of energy in the echolocating clicks, the restricted cone of sensitivity to sound on each side could presumably aid substantially in localizing an echo source especially in view of the common scanning movements of the head during closing on a target.

The conclusion that sound enters the body mainly through the skin of the mandibular region and not via the external ear, although based on experiments with four genera (*Stenella*, *Steno*, *Lagenorhynchus*, and *Tursiops*), needs to be checked in other taxa especially of the larger whales since it cannot safely be extrapolated to all Cetacea.

#### *Specialization for Ultrasonic Clicks*

The second result that should be emphasized is that the response evoked in the mid-brain has a great selectivity for the onset of



**FIGURE 4.** Distribution of sensitivity to sound over the head of *Stenella*. Hydrophone was pressed against the skin at points shown. Numerical values represent attenuation at threshold in dB; therefore, largest numbers represent greatest sensitivity. Contour lines are drawn at intervals of 5 dB in sensitivity. Recording was from inferior colliculus on right (contralateral). Sensitivity was greatest along side of contralateral mandible, under tongue, and on ipsilateral melon. External auditory meatus, not shown, is a short distance behind the eye in the area of least sensitivity (from experiments of ref. 27).

steeply rising sound bursts. Using carefully shaped tone bursts with a variable rise time showed not only a maximal response to the most abrupt rise of amplitude of a tone burst, as is usual in other animals, but also a very rapid decline of response as the rise time is lengthened to 0.5 msec. When it is as much as 5 msec, the sensitivity is decreased nearly 100 fold. Even with slow rise times the response is confined to the beginning of a maintained tone, and there is no response in the inferior colliculus by this method to maintained sound. The evoked potential is purely an on-response and under some conditions of strong stimulation an off-response. This is a remarkable specialization in contrast to the cat and, as we shall see below, the sea lion. We shall note that this sensitivity to rate of rise is combined with the capacity to respond discriminatively to different frequencies even in very brief tones and in the first

fraction of a millisecond of longer tones. But first we must assess the response area.

Figure 5 shows a number of response areas obtained from different experiments and hence different locations in the inferior colliculus. The best frequencies all lie in the region of 50 to 70 kHz, and the upper limit of response by this method and with our equipment was at least as high as 135 kHz. With equipment that is capable of delivering more energy at high frequencies, it might be found that there is response considerably higher. More remarkable is the lower limit since response falls off greatly below 10 kHz and in most experiments no evoked potential could be obtained in the inferior colliculus with the available energy below 6 kHz. Curves of the same shape are obtained in air and in water.

The curve is of the same shape and even has the same position on the ordinate when steeply rising tone bursts of 0.1-ms total dura-

tion are compared with 1-msec or longer tone bursts. This says that the response to the abrupt onset, which itself is equivalent to a wideband noise burst, does not obscure the specific effect of the frequency contained in the brief tone burst since that frequency determines the high threshold at very low and very high frequencies and the minimum threshold at the best frequency. The response area by the evoked potential technique agrees remarkably well with that measured by behavioral methods by Johnson (ref. 44) in respect to best frequency, upper limit, and approximate dB/octave decrease in sensitivity on each side of the best frequency.

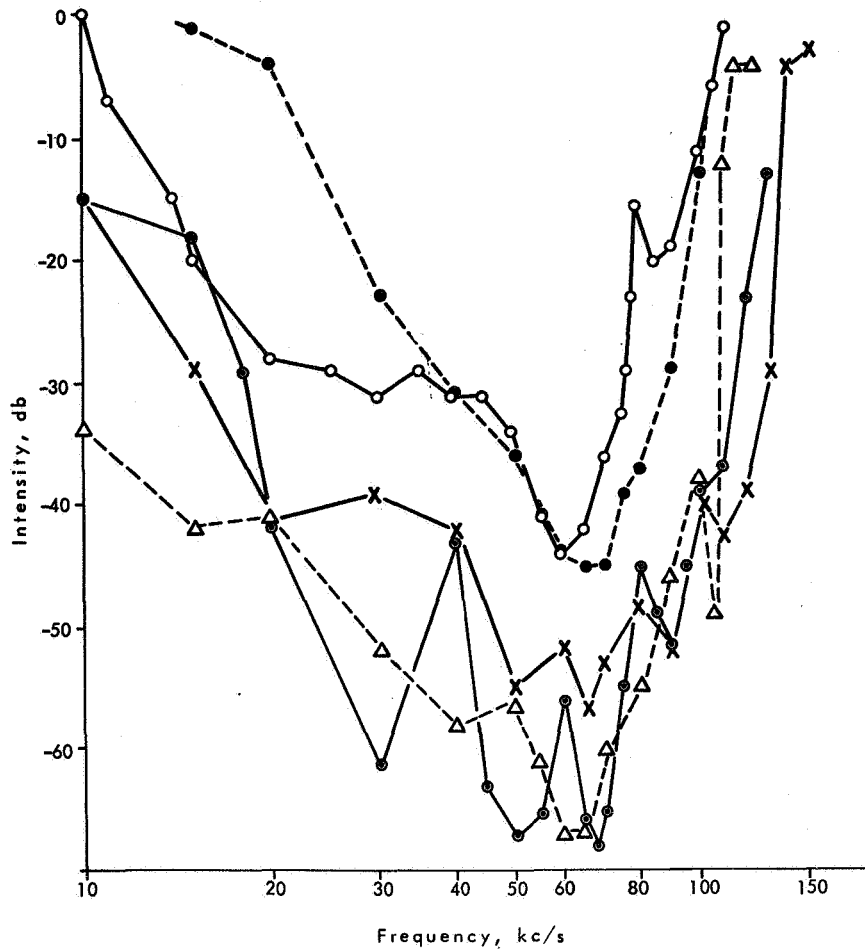
The high best frequency, the very low sensitivity below 6 kHz, the high selectivity for rapid rates of rise of the onset of sound, and the insensitivity to slowly rising or maintained tones are strong indications of specialization of this part of the auditory system for ultrasonic clicks of the echolocating type. The abundant repertoire of whistle-like sounds believed to be important in social communication are chiefly lower in frequency and slower in rise time than our collicular responses demand. (The absence of evoked potentials to slowly rising sound cannot readily be attributed to poor synchronization of units alone, although of course this is possible. The rise times are only a very few milliseconds and elicit good evoked potentials in other animals including sea lions (see below). The number of animals and electrode locations sampled make it unlikely that we have missed a major region of the auditory midbrain, although of course this is possible, too.) One must conclude that the processing and analysis of the low frequency, slowly rising social communication whistles are mainly done elsewhere, presumably at higher levels like the cerebral cortex, and that somehow the streams of impulses for such stimuli get through the midbrain en route to the medial

geniculate and cortex too asynchronously or diffusely to produce any substantial evoked potentials. We will return to this remarkable evidence of specialization again below.

Turning to other properties of the responsiveness of the inferior colliculus as indicated by its evoked potentials, it is noteworthy that one can easily detect changes in this sign of response to changes of intensity of the sound delivered by as little as 1 dB. Frequency discrimination is also quite sharp, and in some portions of the range a 3-dB change in effectiveness of a stimulus can be caused by a 1 percent change in frequency of the carrier wave in a brief sharply rising and falling burst. Very likely this function is much steeper yet for certain classes of single units.

The response to a given frequency and intensity is markedly altered by the existence of a background tone of another frequency and intensity, especially if these are not far apart or if the background sound is a white noise. Even if it is an octave or more from the brief test tone, there can be a pronounced interaction which is sometimes in the direction of "masking" (i.e., of decreased response to the test tone) and sometimes the opposite, actual enhancement. This relation is complex and frequency specific. The strongly depressing action of white noise raises a serious question as to how the porpoise retains its sensitivity in rapid motion through the water. This rapid motion might be causing masking noise due to turbulence. Perhaps there is a specialization in streamlining and in textural adaptation of the surface of the skin for reduction of such turbulence; if so, the reduction of masking sound may be one of the main achievements of such specialization.

Figure 6 shows that even more effective as stimuli than short pure tone bursts are frequency modulated bursts of the same duration, intensity, and rise time. Over a wide

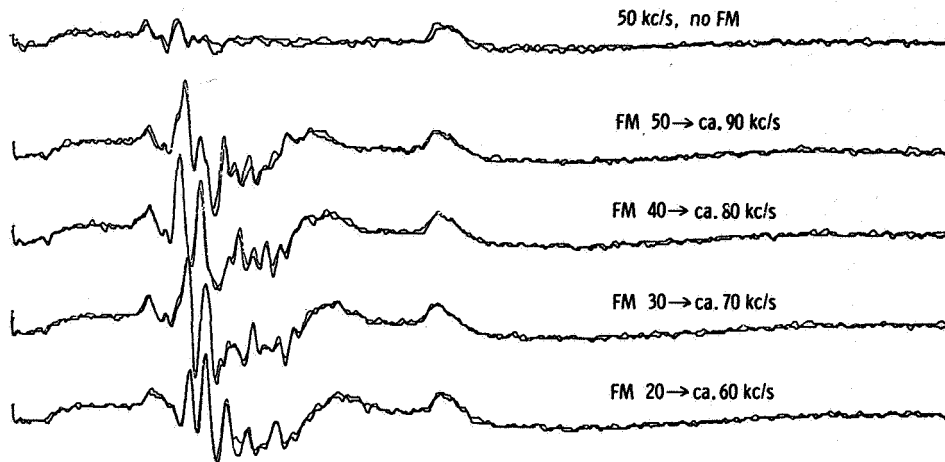


**FIGURE 5.** Sample audiograms from several *Stenella* made by eye-estimated threshold of evoked potential at each frequency. Intensities are referred to an arbitrary maximum intensity. The peaks of low sensitivity in individual curves are real and presumably represent a patchy or topographically segregated distribution of nerve cells of different response area. Our electrode samples a limited population of cells (ref. 27).

range of frequencies, both ascending and descending, FM typically gives a much stronger evoked response than any pure tone contained in that frequency sweep. Moreover the form of the evoked potential is greatly altered by relatively modest changes in the starting and ending frequency, that is, the span of the FM tone burst. It is not yet

known how short a burst or small a span is adequate or what is the optimal stimulus. It is only certain that a small fraction of the FM sweep offered in such an experiment as that of figure 5 is sufficient and has already determined the characteristic shape of the evoked potential for that span.

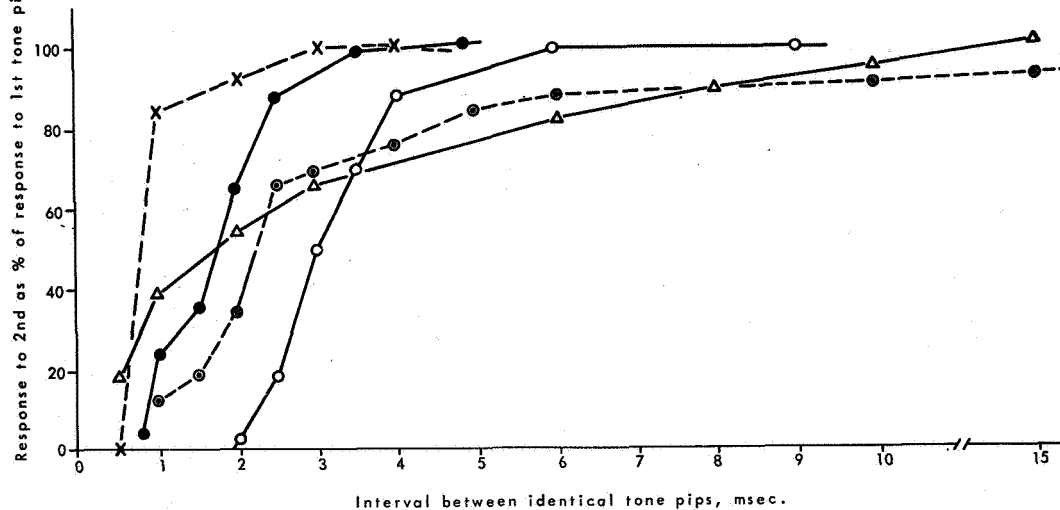
Recovery of the responsiveness as tested



**FIGURE 6.** Frequency modulated tone bursts are more effective than pure tone bursts. Stimulation by tone bursts 3 msec in duration with 0.5 msec rise and fall. Actually less than 1/10th of this duration is effective, and waveform of evoked potential is determined by a correspondingly small fraction of the 40-kHz range. One hundred-twenty-eight sweeps computer-averaged for each line; two averages superimposed. Time of full sweep equals 32 msec (ref. 27).

by a second stimulus following a first or conditioning stimulus is another sign of specialization for the early echos from nearby objects. Figure 7 shows a sampling of recovery curves from different electrode locations in different experiments. Some show much more rapid recovery than others; evidently some parts of the inferior colliculus are able to show appreciable response within much less than half a millisecond after a previous, nearly maximal response. Figure 7 is based on estimated percentage recovery of a certain landmark in the complex evoked potential form. The actual recovery can be pushed even earlier by computer averaging and subtraction of the response to the conditioning tone alone from the response to the conditioning followed by the test tone. This method shows that there is a small but distinct complex response to the test tone superimposed on that to the conditioning tone even when the silent period between the two 0.1-ms, abruptly rising tone bursts is itself

only 0.1 msec. That this is a real recovery is shown by the control in which the silent period is reduced to zero so that we compare a 0.2-ms tone burst with a 0.1-ms tone burst. As expected from the comments previously about the response being essentially an on-effect, there is no appreciable difference between the 0.1- and the 0.2-msec tone bursts. Merely introducing a silent period of 0.1 msec allows sufficient recovery that a new on-response is appreciable and has a complex form, only somewhat simplified from that of more fully recovered responses. We have done experiments where the conditioning tone was nearly maximal in intensity and the test tone many dB lower, as must occur in natural echos. In this case the recovery is significantly slower but is still rapid. Moreover the curve of recovery can have a different form, with some special dips not seen when the test tone is of higher intensity or when it is equal to the conditioning tone (fig. 8).



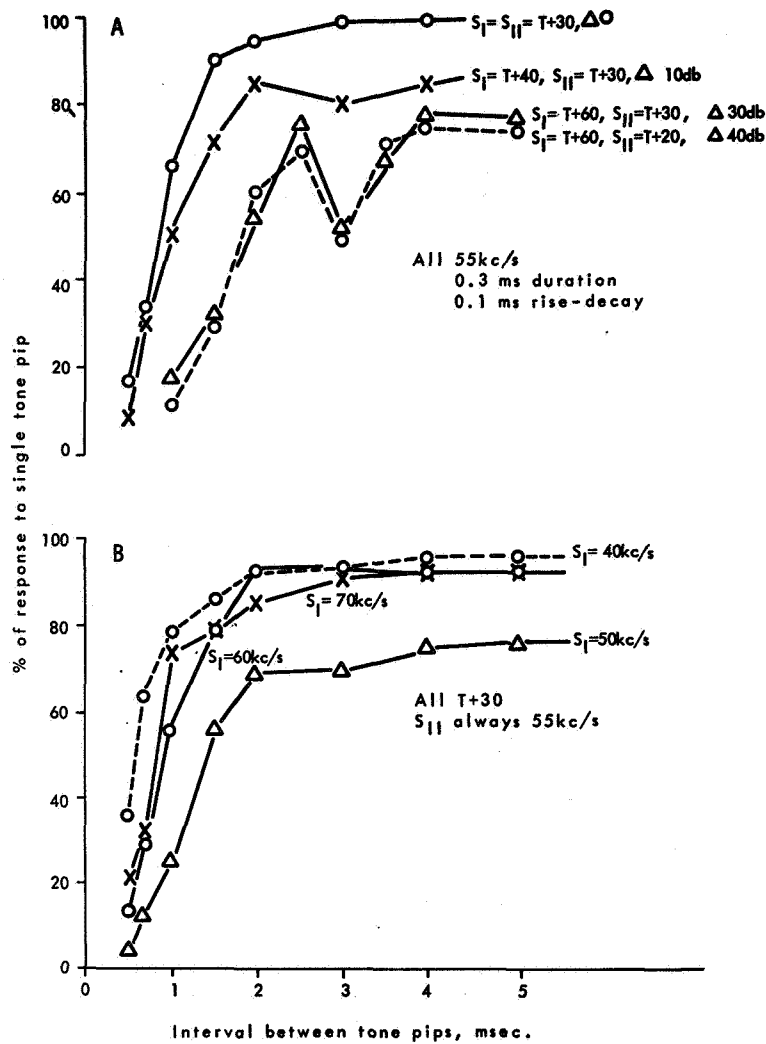
**FIGURE 7.** Representative recovery curves of collicular evoked potentials in *Stenella*. Two identical tone bursts of approximately 0.5 msec duration and 0.2 msec rise and decay time were given at intervals from 0.5 to 15 msec. Size of the response of certain component to the second of these is plotted as percentage of response to same stimulus alone. Different recording sites show quite different recovery rates, but some are nearly complete in less than 1 msec (ref 27).

*Recording with Implanted Electrodes in  
Alert, Trained Porpoises*

All these properties were shown in the anesthetized animals and most of them repeated and confirmed in the unanesthetized, alert, and cooperating animal, as expected from the fact that our anesthesia for the previous work (ref. 27) was a combination of nitrous oxide and halothane. In humans this combination gives complete amnesia for the operation and analgesia, so that the patient does not complain of pain but does understand and respond to commands by the surgeon during the operation.

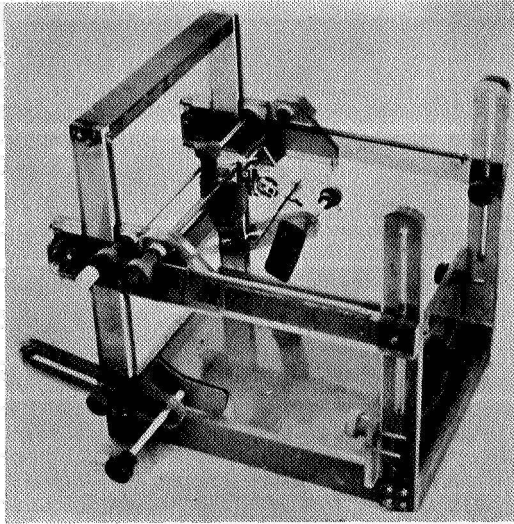
Still, recording from the unanesthetized and cooperating animal has several justifications besides confirming this expectation. The main one to be reported here is that such an animal, having been trained to do so, can

upon command emit a series of clicks like those used in certain kinds of normal echolocation. This gives us the opportunity to study whether the responsivity of the auditory system is in any way different when the animal emits the conditioning clicks voluntarily and hence "knows" when a conditioning sound is going to occur. Furthermore it knows that it will be loud and brief and will probably be followed within a short time by a faint but biologically significant echo. This is potentially a different situation from that we have been describing, in which the conditioning tone is delivered by us at an arbitrary time. The arbitrary time is not entirely unknown or unexpected; if under the conditions of nitrous oxide and halothane the porpoise brain is able to notice, it may perhaps be anticipating the clicks being delivered from our loudspeaker or hydrophone because they are com-



**FIGURE 8.** (A) Recovery of responsiveness to fainter second stimulus in collicular evoked potentials from *Stenella* with tone bursts of the same frequency (55-kHz, 0.3 msec duration, 0.1 rise and decay times). Recovery of response to the second of the two stimuli plotted as a function of interval, when the stimuli were of equal intensity (30 dB above threshold or  $T+30$ ), and when the first was 10, 30, and 40 dB louder than the second. Note that although a louder first stimulus does prolong the depression of the second response, recovery is still considerable at 2 msec interval when the first is 40 dB more intense. Note also the dip in recovery curve at 3 msec, presumably representing short-term inhibition superimposed on refractoriness of receptor elements. (B) Comparable measurements showing responsiveness to a 55-kHz signal following exposure at different intervals to an earlier stimulus of 40, 50, 60, and 70 kHz. Both stimuli in the pair were chosen to be 30 dB above threshold at their respective frequencies (ref. 27).



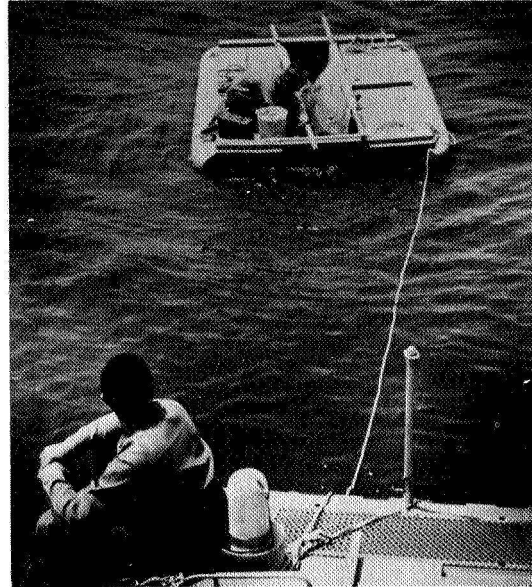


**FIGURE 9.** Stereotaxic device for porpoises, designed at Point Mugu Marine Bioscience Facility. Porpoise's head enters device from left and is centered and leveled around longitudinal axis by eye. Having chosen the point of entrance relative to surface landmarks like the blowhole, device permits drilling at chosen angle.

ing with regularity at a repetition rate well within his normal range, commonly 50/sec.

The implantation of the electrode arrays for chronic preparations is done, usually one on the right and one on the left, each with seven or 18 electrodes spaced from 4 to 10 mm apart along a common shaft. This is the step that requires our stereotaxic device (fig. 9) together with surgery under halothane anesthesia (ref. 45) and X-ray monitoring of the position of the electrode.

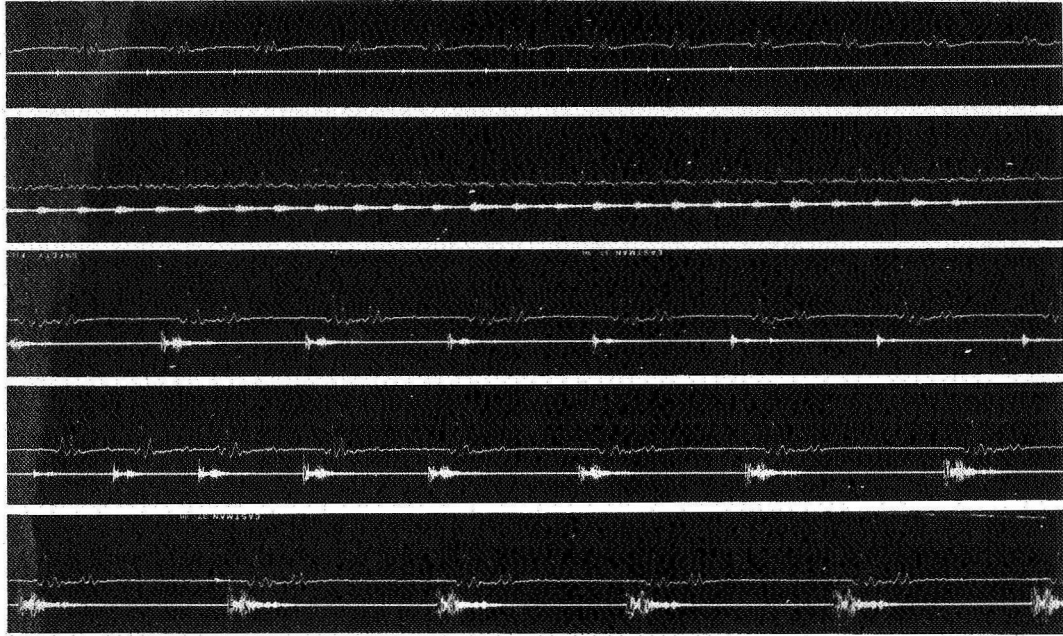
Figure 10 shows the animal lying quietly in a sling so that its acoustic environment will be relatively constant, and after hydrophones have been fixed by suction cups to the skin and telemetering transmitters for the brain potentials similarly attached. The recording has usually been done in artificial pools on shore which with high intensity sounds have a complex pattern of reverberation and echo that forms the background on



**FIGURE 10.** Chronically implanted unanesthetized cooperating and trained porpoise (*Tursiops*) lying in a sling in float tethered to research vessel well off shore. Receiving and transmitting hydrophone are attached by suction cups below the water level. Amplifiers held by suction cups above water telemeter the brain potentials to receivers on research vessel. Trainer calls for a series of echolocating clicks when desired (photo courtesy of Pt. Mugu Marine Bioscience Facility).

which alterations due to our stimulus conditions are superimposed. Some of the experiments have been done at sea with the animal floating in its sling tethered some meters away from the laboratory vessel carrying the sound generating and recording equipment. There are still many echos under these conditions, but they are far fewer and for the most part delayed sufficiently to be after the epoch of interest for our recordings.

Figure 11 shows the evoked potentials in the inferior colliculus of an unanesthetized, cooperating, and trained animal in response to his own voluntarily emitted clicks. Such records have shown among other things a remarkable lack of parallelism between the



**FIGURE 11.** Evoked potentials (*upper trace*) from inferior colliculus or vicinity in an alert, cooperating, trained porpoise (*Tursiops truncatus*), implanted several days before, with 14 electrodes, in two linear arrays or assemblies, one left and one right, each of 7 fine wires emerging and bared at staggered intervals of 5 mm from an insulated hollow needle. Running film record from magnetic tape of the experiment. Brain potentials are responses to sounds produced voluntarily by the porpoise and recorded by a hydrophone (*lower trace*). Note that some low amplitude sounds produce sizeable evoked potentials and some high amplitude sounds small potentials. Shown are non-consecutive samples from several different click trains. Each line is 200 msec long.

variations in amplitude of the emitted clicks as seen by a fixed hydrophone and of the recorded evoked potentials. Some very intense clicks of the long (1 to 2 ms) type are accompanied by modest evoked potentials. Many feeble clicks, 20 dB weaker, of the short (0.06 to 0.2 ms) type evoke good brain responses. It appears that some component of the emitted clicks is important for the response in the inferior colliculus and that this component does not vary in amplitude *pari passu* with the variations in overall intensity of the click.

If we compare the size of the response to

a voluntarily emitted click with that to a sound we deliver of the same intensity as seen by a hydrophone near the head, the latter is a much smaller evoked potential. From our experience with different kinds of sounds we believe this discrepancy cannot entirely be attributed to the quality of the porpoise's own click, but we cannot be certain of this. Presumably, therefore, we are seeing a more effective click due to its greater intensity inside the head. This would be evidence, no stronger than the certainty of the exclusion just proposed, that the inner ear and the sound guide to it are not perfectly isolated

acoustically from the sound-generating parts of the head (refs. 40 and 41). Therefore, we cannot tell whether the response to his own clicks embodies some self-protection from the expected loud sound.

When we use the animal's voluntary click, as recorded in a hydrophone close to the head, to trigger our sound generator to deliver a test sound from another hydrophone acting as a loudspeaker, we can test the responsiveness at chosen delays after the animal's own click with what amounts to artificial echos. They have the important advan-

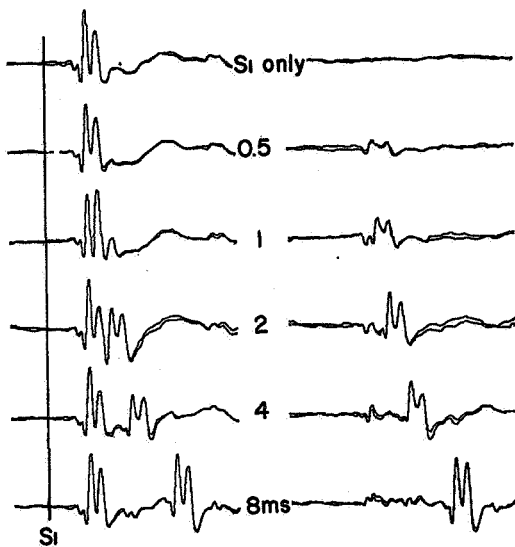


FIGURE 12a. Rate of recovery of evoked potentials from an animal and electrodes like those in preceding figure. Computer-averaged records. Experiment shows recovery after a response to a "conditioning" stimulus (S1), as revealed by response to subsequent "test" stimulus (S2), after different delays. Upper: S1 and S2 are both artificial tone bursts of 50-kHz, 0.2 msec duration, abrupt rise and fall, about 30 dB above visible evoked potential threshold, without averaging. Two independent averages of 32 sweeps each are displayed. On left are records of both S1 and S2 responses; right are results of subtracting the S1 response alone from each of the pairs, to uncover the component attributable to S2.

tages over natural echos that the test tone burst is constant in form, composition, and intensity whereas the natural echos are inconstant both because of variations in the outgoing click and because of slight movements of the head or of the target. Figure 12 shows one such experiment with artificial echos at various intervals. The principal result is that in comparison with the recovery of responsivity following conditioning sounds delivered arbitrarily by us, recovery is not greatly different under our conditions. There is no supernormal or facilitated period, but recovery

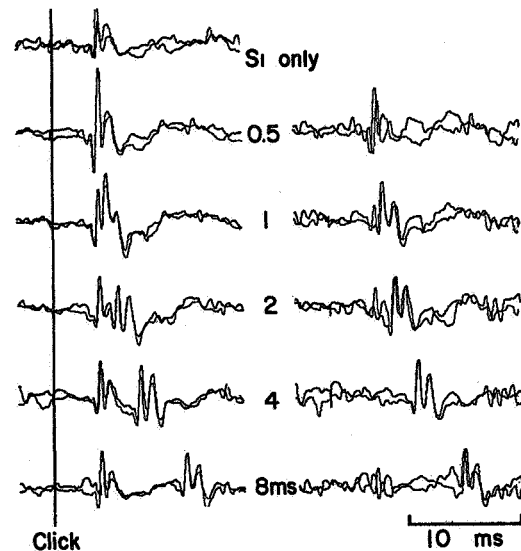


FIGURE 12b. S1 is a click in the porpoise's own train of echolocating clicks, spontaneously emitted when a fish is tossed into the pool 2 m from his snout; clicks used here are one of his very brief, medium intensity type, the single main wave having a duration of 0.1 msec. S2 is an "artificial echo," like the tone bursts of the upper half. Successive porpoise clicks triggered the sequence, 0.5, 1, 2, 4, 8 msec delay and no S2, over and over to provide records for averaging. Two independent averages of eight sweeps each are displayed. Comparison, especially at 0.5 and 1.0 msec, indicates better recovery following porpoise's own click, though it may help that click and test echo are not identical sounds.

is at least as good, perhaps somewhat faster, following the animal's own voluntary click. This is cautiously stated because we cannot compare conditioning bursts exactly matched in quality or even in intensity with porpoise clicks, since the latter reach the ear partly through the head. But the extremely conservative comparison of equal conditioning and test tones with porpoise clicks causing substantially larger evoked potentials than the artificial echo sound by itself shows no less but apparently more recovery at the earliest interval of 0.5 msec after the porpoise's own click (fig. 12).

It will be interesting to pursue these matters also in the case of high repetition rate clicking by the porpoise when echos from objects 2 or more meters away will be returning, not in the interval between that click and the next but in a subsequent interval (refs. 32 and 46). Insofar as the repetition rate of clicks rarely exceeds 500 to 700 per sec and recovery is very well along though not complete in that interval, it is quite feasible physiologically for echos to be analyzed during the high frequency buzzes or squeals. Figure 13 shows a sample of such a buzz and of other epochs when sounds of different kinds occurred. Note that many kinds of sounds including the porpoise's own whistles do not cause evoked potentials in our electrodes, emphasizing once more the specialization of this region of the auditory system for echolocating clicks. On present evidence it seems reasonable physiologically that the porpoise can measure distance and at the same time evaluate the character, size, and location in space of an echoing object (ref. 47).

*Evoked Potentials from the  
Cerebral Cortex in Porpoises*

Finally it should be reported that although we have made no systematic study of

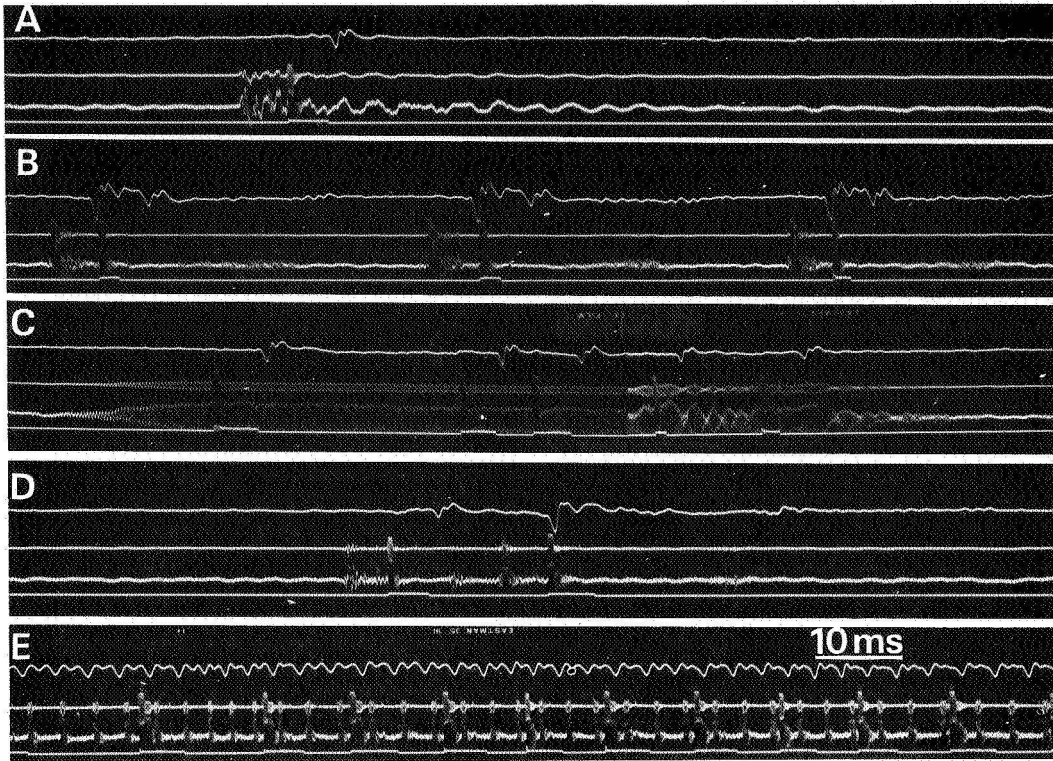
the responses from the cerebral cortex, on a few occasions we recorded from a cortical site far ventrally and laterally and obtained responses to sounds quite different from those in the colliculus. Slowly rising and maintained sounds as well as low frequency tones extending below 1 kHz elicited good responses similar to familiar cortical-evoked potentials, and the best frequency was about 5 kHz. It appeared that we had found the missing portion of the auditory system specialized for analysis of the low frequency social communication whistles that cause little or no response in the colliculus.

*AUDITORY EVOKED POTENTIALS  
IN PINNIPEDIA*

Because they belong to quite a different order of mammals and yet face the same problems and opportunities in the aquatic environment as do porpoises, we have made a parallel study of a series of ten sea lions (*Zalophus californianus*).<sup>4</sup> The basic technique was the same as for the porpoises. We used chiefly barbiturate anesthetized animals since these species do not lie so quietly or tolerate attached loudspeakers or hydrophones so well as porpoises. From data on cats this anesthetic should exert little or no effect upon evoked potentials at the level of the midbrain. We have done some experiments on unanesthetized, restrained sea lions however and have seen no difference in the results. Recording and stimulation have been done in air and under water with no obvious differences.

The results of principal interest are the following. The upper limit of frequency to which evoked potentials could be obtained with the intensities of sound available was 30 to 40 kHz in different experiments. This con-

<sup>4</sup>BULLOCK ET AL., *loc. cit.*



**FIGURE 13.** Evoked potentials (*upper trace*) from an animal and electrodes like those in figure 11. Running film record from magnetic tape of the experiment. Two *middle traces* are hydrophone outputs at low and high gain showing “artificial echos” or test tone bursts (marked by the ON of the square wave in *lower trace*) delivered at chosen intervals after trigger pulse produced by onset of porpoise’s own echolocating clicks (*B, D*) or by some other sound (*A* and *C*). *A* shows that a sound of low frequency (second and highest deflection = about 4 kHz) relative to the clicks and test tones (main energy about 20 and 40 kHz, respectively) is ineffective in eliciting an evoked potential; single evoked potential in this line serves as a control—the response to the test tone alone. *B* shows three clicks of high intensity, long duration ( $>1$  msec) type, followed by “artificial echos” after 6 msec. Evoked potentials follow both sounds with a latency from hydrophone deflection to collicular deflection of 4 msec and show complete recovery of responsiveness (compare *A*). *C* shows that the porpoise’s own social communicating whistles (about 3 to 6 kHz) do not evoke any potentials or seriously mask response to test tone. *D* shows an ineffective sound of too low a rise time and frequency, followed by effective test tone, and effective click followed by poorly recovered test tone response. *E* is sample of high repetition rate clicking (“rusty hinge” sound; 250 to 350 clicks per sec) with intermittent test tone bursts; these are followed at the expected time (4 msec) by partially recovered evoked potentials superimposed on those to the clicks. This is the situation during high resolution discrimination by the animal of targets close by, though with echos that follow every click. The test tone, though higher in amplitude, is not as effective as a porpoise click (or its echo) presumably because it does not have the best frequency-succession (FM); it is a 40-kHz tone, 0.6 msec long, rising and falling abruptly, about 30 dB above visible evoked potential threshold without averaging. Each line = 125 msec.

trasts with Mohl's figures (refs. 48 to 50) of 64 kHz or higher for the seal (*Phoca vitulina*) by behavioral end point (ref. 51). The evoked potentials in the inferior colliculus in sea lions respond maximally to abruptly rising tone bursts but decline relatively little as the rate of rise of the tone burst is lengthened. Excellent responses are obtained with 50 msec and even slower rise time. The response is still chiefly a transient one however. There is no marked advantage in effectiveness of frequency modulated stimuli over pure tone stimuli whether upward or downward. The best frequency is below 5 kHz, and responses have been obtained as low as we have looked, which is about 0.6 kHz. The frequency and intensity discrimination is not nearly as good as in the porpoise. Recovery of response after a conditioning tone is appreciably slower than in porpoises and appears similar to that reported for cats. Typically 50-percent recovery is obtained by 2 or 3 msec. With protracted averaging of several hundred responses and computer subtraction of conditioning response from conditioning plus test response, it is possible to see a small response to the test click when only 0.2 msec of silence has occurred since the conditioning click. There is very little directional sensitivity (ref. 52), and the response is obtained in all 360° in the horizontal plane around the head with only an advantage of about 10 dB for a hydrophone held 10 cm lateral to the contralateral external ear, over the least effective positions which are almost equally behind the head, straight in front, and to the side of the ipsilateral ear. These figures are of course very rough and depend on many factors in the stimulus situation but serve to emphasize their dramatic difference from the porpoise's limited cone of receptivity with its best direction not to the side but only 10° or 15° from the midline straight ahead.

In sum, the pinnipeds examined have

auditory responses like those of a cat gone to sea with little evidence of porpoise-like specialization. This agrees with the report of Alderson *et al.* (ref. 53) on the cortex of *Phoca*. The inferior colliculus, of course, responds very well to sharp clicks such as would be particularly favorable for echolocation and have been reported by some observers to be emitted on occasion by sea lions, but their system cannot take advantage of ultrasonic frequencies, of frequency modulation, or of small differences in frequency to nearly the same extent as can porpoises. Nor is the inferior colliculus as clearly specialized for brief high frequency clicks as it is in porpoises, but it responds quite well to low frequency, slowly rising sounds such as those involved in social communication.

#### COMMENT AND FUTURE PROBLEMS

These studies on porpoises and sea lions bring out aspects of specializations that distinguish the two groups in auditory analysis of sounds. The specializations help to explain how the fantastic achievements of the porpoise in recognizing and localizing small targets of very slight difference in echoing quality (refs. 54 and 55) can be understood in neurophysiological terms. It is not possible on these purely physiological data to pronounce on the question, still debated in the literature, whether sea lions and other pinnipeds use echolocation. We can, however, say that sea lions are relatively unspecialized compared to porpoises.

Dr. Griffin likes to ask why we can't do what a bat or a porpoise can do. If our own system is more like a cat's and hence a sea lion's, these findings on central specialization help to explain it. Nevertheless many questions remain to be investigated. For example, what electrophysiological signs and measures can be found of ability to localize echoing



objects, static or moving, and are they specialized compared to ordinary mammals? Is there any neural facilitation of expected echos? Are middle ear muscle reflexes employed to depress responses to the animal's own outgoing click and yet be ready for early returning echos in the rapidly sound conducting aquatic medium? For what does a porpoise need the tremendously enlarged inferior colliculus; what can he do that requires so many neurons? The inferior colliculus alone is larger than a whole bat's brain, indeed nearly as big as some small bats. What is the function of the inferior colliculus in the baleen whales that apparently lack the ultrasonic click emissions and presumably the fine grained echolocation of the porpoises and toothed whales? What types of units account for the responses in the inferior colliculus of porpoises, and how do they differ from those in cats and sea lions? What happens in the medial geniculate? Where and how extensive is the auditory cortex in toothed and in baleen cetaceans, and how is it organized and specialized compared to cats and other laboratory animals?

The studies reported show that, given the specimens and the facilities, the techniques are now perfectly practicable to anticipate resolution of all these problems.

#### SUMMARY

Recent work is reviewed, chiefly on porpoises, showing peripheral auditory and central neurophysiological specializations favorable for the analysis of echolocating clicks and their echos.

As seen in the cochlear potentials as well as in evoked potentials of the midbrain, the upper limit of reception extends at least to 135 kHz and possibly higher. Best frequencies for evoked potentials in the midbrain are in the range of 50 to 70 kHz.

Sound is received mainly through the skin of the mandible, and the sensitivity over the external auditory meatus is very much less and no better than surrounding areas of the head. A region of somewhat less sensitivity than the mandible but higher than elsewhere is over the melon. There is a restricted cone of receptivity extending forward and downward, with a center  $10^\circ$  or so from the midline of the head and falling off steeply so that sound from a source  $45^\circ$  to the side may be 20 to 30 dB less effective.

One of the auditory stations, the inferior colliculus, is enormously hypertrophied and from its evoked potential highly specialized for rapidly rising sounds of high frequency and short duration. It has given all the response it will to a tone burst of less than 0.1-msec duration, but longer durations give no greater response. It is extremely sensitive to the rate of rise in the 0.05- to 2-msec range, and a tone of 5-msec rise time is nearly one hundred fold less effective than an abrupt tone. In spite of listening for such a short period, the inferior colliculus makes extraordinarily fine frequency and intensity discriminations. It responds better to frequency modulated than to pure tones, again discriminating sharply between slightly different FM tones. It is strongly and complexly subject to interactions with other tones in the background, some of which mask and some of which actually enhance the response. Recovery is very rapid even when the second or test sound happens to be very much weaker than the first.

The evoked potential from the midbrain sites studied is remarkably insensitive to low frequencies (below 6 kHz) and to slowly rising amplitude (above 5 msec). It manifests a system highly specialized for echolocation clicks. The slower and lower sounds like those in porpoise whistles do evoke responses in the cerebral cortex.

These properties have been confirmed in unanesthetized, alert, and cooperating animals with implanted electrodes. This technique has permitted recording the evoked potentials in response to the animal's own voluntarily emitted echolocating clicks delivered both in response to objects of interest like fish thrown into the water and after training to deliver clicks in response to the trainer's command. Such evoked potentials suggest that some component of the click is most effective in eliciting these responses—a component that does not necessarily vary in proportion to the overall intensity of the click. They also suggest that the inner ear and its sound path are not perfectly isolated acoustically from the sound generating parts of the head since the evoked potentials are much larger than those to artificial sounds of the same intensity as seen by a hydrophone near the head of the animal.

Extending this technique to use the animal's voluntary echolocating clicks, picked up by a hydrophone, to trigger a sound generator that delivers an artificial echo after a chosen delay has permitted examining the recovery of responsiveness to the standard test tone as a function of time after the outgoing voluntary click. Recovery is found to be at least as rapid as for artificial sound, probably more rapid, but no facilitation has been seen under our conditions.

In all these respects the responses obtained in a comparable way from the sea lion show much less specialization for clicks and their echos. The responses of the sea lion are very much like those of cats. The upper frequency limit of sensitivity is between 30 and 40 kHz with available intensities.

Other vertebrates and invertebrates are still too little known to make meaningful statements on the neurophysiological properties that might be relevant to any echolocation of which they are capable.

#### ACKNOWLEDGMENT

This investigation has been supported by grants to T. H. Bullock from the National Institutes of Health, National Science Foundation, Air Force Office of Scientific Research and the Office of Naval Research. The Naval Undersea Research and Development Center supported S. H. Ridgway.

#### DISCUSSION

NORRIS: Have you seen any evidence in the records of the animals hearing their own signals as they are emitted, and before they return as echoes?

BULLOCK: Frequently. They respond to their own sounds. The first big wave that you see is a response to his own sound. Of course, I can't say whether that is mediated through the water or whether he is just getting the sound in the inner ear before it ever gets out to the water. What we are particularly interested in is whether the animal is perhaps quite insensitive to this, or at least less suppressed by the loud outgoing sound when he does it himself. He knows when it is going to happen, knows that it is going to be loud, and knows that it is going to be brief.

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