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The Cetacean central nervous system

Sam H. Ridgway

Whales, dolphins, and porpoises, 78 species of entirely aquatic mammals, comprise the order Cetacea whose distant ancestors, according to paleontologists, left land in the early Eocene about 55 to 60 million years ago. The Odontoceti (toothed whales, presently 67 species) and the Mysticeti, 11 species of baleen whales, have evolved separately since at least the late Eocene. Modern cetaceans are diverse; the largest blue whale is some 60,000 times heavier than the smallest newborn porpoise. Average adult size among cetaceans varies by at least 1000 times. Small and large species occupy all oceans from the equator to the polar seas, some forms also inhabit rivers, and four species live only in fresh water.

1. Brain size, growth, and shape

Brain size among adult cetaceans ranges from about 200 g in an Indus River dolphin or a La Plata dolphin to a record high of 9,200 to 9,300 g reported for the largest male sperm and killer whales. Although adult male sperm whale brains average about 7,800 g, the dolphin family (Delphinidae) seem to have reached the apex of cetacean brain:body ratio; with body size near the same range as humans and brain weights approaching those of the human brains – *Tursiops* (Figure 1) about 1,500 g. *Steno* circa 1,400 g, and *Lagenorhynchus* around 1,300 g.

At birth, bottlenose dolphin's (*Tursiops*) brains are about 42% of adult size, reach 80% by weaning-age at 18 months to two years, and full development by age eight or ten.

In the embryonic stage, the dolphin brain, like that of other mammals, is longer than wide. By the late fetal stage, the odontocete brain is globular in appearance, wider than long (Figure 2). In postnatal mysticete brains, length and width are more similar. A dolphin brain viewed from the medial aspect of a sagittal section (Figure 3) shows that the height is also great compared with the length. An S-shaped curving of the neural axis leaves the axis of the forebrain almost perpendicular to that of the midbrain, giving the impression that the forebrain rotated ventrally during development.

The cerebral hemispheres of Cetacea are large and enormously convoluted. Odontocetes exceed humans, and all other groups, in the complexity of the cerebral cortical pattern of gyri and sulci. A larger percentage of the dolphin cortical surface is buried beneath the surface of each cerebral hemisphere. The main sulci that arch along the dorsolateral cerebral surface are deep and incised with microgyri. Deep to the sylvian cleft lies

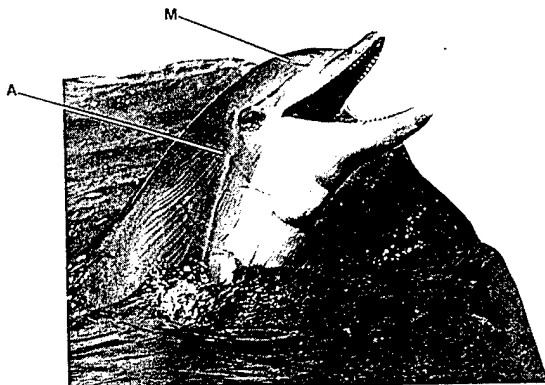


Figure 1. Right side of head, Bottlenosed dolphin *Tursiops*. A = vestige of external auditory meatus, M = melon.

an extremely large insula consisting of radial gyri arising fan-like from the transverse insular gyrus, and covered completely by the frontal, parietal, and temporal opercula. In a series of *Tursiops*, mean cortical surface area was 3745 cm² compared with 2275 cm² in a series of human brains; however, the dolphin's cortex was thinner (1.3 to 1.8 mm), and the total volume of cortex was about 80% of that found in humans.

2. The cerebral cortex

Some histologists suggest that the whale cortex as a whole, while vast in surface area, does not appear to have reached the ultimate stage of cortical evolution and retains some conservative characters seen in primitive forms such as hedgehogs and bats. Cortical layer I contains extraverted dendrites from neurons of layer II. Layer IV is incipient or at least hard to identify (perhaps with the exception of immature brains). With the absence of a typical layer IV, thalamocortical input to sensory cortex may be mainly to layer III based on cytochrome oxidase and GABA staining. Areas of cortical surface identified as primary sensory cortex by physiological mapping studies are agranular and not distinguished as primary sensory cortex on histological grounds. It has been suggested that during evolution, cetaceans have preserved features of "initial" or "archetypal" brains of primitive mammals to a much greater extent than have the great majority of modern land mammals. A long period of evolution

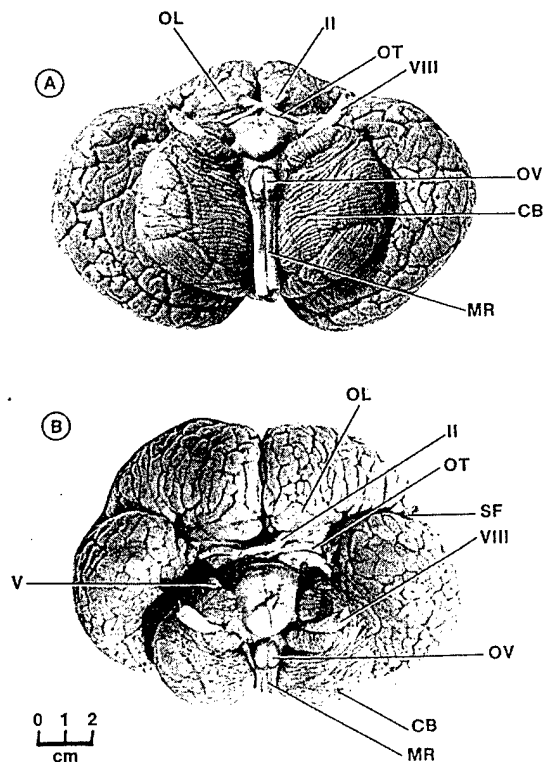


Figure 2. (A) Postero-ventral and (B) Antero-ventral views of a neonate dolphin (*Tursiops*) brain. The dura, blood vessels, and most cranial nerves have been removed. Neonate brains averaged 42.5% of adult weight. OL = olfactory lobe, II = optic nerve, OT = optic tract, VIII = auditory nerve, OV = olive, CB = cerebellum, SF = sylvian fissure, MR = median raphe, calibration mark is 1 cm.

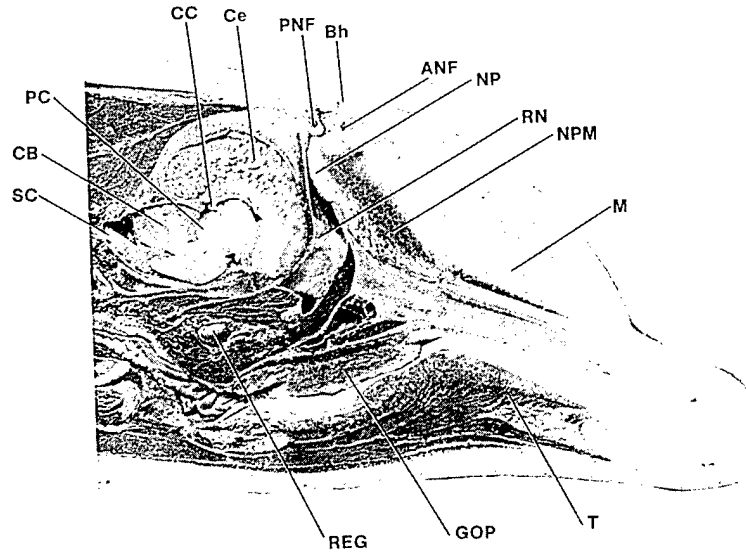


Figure 3. Sagittal section, about 1 cm to the right of median raphe of the brainstem. T = tongue, GOP = glandular region of oropharynx, REG = right side of epiglottis, SC = spinal cord, CB = cerebellum, PC = posterior (inferior) colliculus, CC = corpus callosum, Ce = cerebrum, PNF = posterior nasofrontal sac, NP = nasal plug, RN = right nasal cavity, NPM = nasal plug muscle. M = melon.

in a completely aquatic environment has often been cited as a major factor in the development of cetacean brain characteristics; however, when making such suggestions one should keep in mind that the Sirenia have also been totally aquatic for 55 to 60 million years and their brains are radically different – relatively small and lissencephalic with a thick, highly laminated isocortex. Sirenia are slow plant eaters in contrast to the most encephalized of the Cetacea which are fast upper food web predators.

According to at least two studies, the ratio of glial cells per nerve cell is correlated directly with brain size. There is at least a 20-fold decrease in neurone density from mouse to whale. Regressions of neurone density have a decreasing slope similar to the decreasing slope of regressions of corpus callosum size among delphinid cetaceans emphasizing a likely connection between the relatively small cetacean corpus callosum and neurone density.

3. The brain blood supply

In *Tursiops*, *Delphinapterus* (the white whale), and *Monodon* (the narwhal), and very possibly in all cetaceans, connecting vessels that make up the circle of Willis in most mammals are absent. The subdural blood supply for each hemisphere is completely independent. Neither the internal carotids nor vertebral arteries supply blood to the brain. There is no vertebro-basilar system, and the internal carotid terminates at the ear without entering the cranial vault. The entire cerebral blood supply comes through a massive thoracico-spinal rete supplied by intercostal and posterior thoracic arteries. Different from the usual form in mammals, the dolphin blood-brain barrier comprises both endothelial and glial cells forming two concentric rings separating blood from brain parenchyma.

4. The olfactory apparatus

In early fetal stages of both mysticetes and odontocetes, the olfactory bulb, nerve, and tracts are present. As the fetus develops, these structures degenerate and are completely absent from mature odontocete brains. Olfactory tracts, but not nerves or bulbs, are found in at least some adult mysticete brains.

Although the more peripheral olfactory components of the cetacean nervous system are absent or rudimentary, other brain structures traditionally thought to be involved in olfaction are present in the mature dolphin. The olfactory lobes and septal areas are large, the hippocampus and subiculum small, the well developed entorhinal cortex more anteriorly located in the temporal lobe, and the presubiculum more posterior than in other mammals; however, in general, the rhinencephalon displays the same basic structural arrangement as in primates or carnivores. The seemingly paradoxical presence of a "nosebrain" without peripheral connections or sensory olfactory endings is one of the more interesting features of the cetacean central nervous system.

The tiny terminal nerves that accompany the olfactory nerves in many vertebrate species are present both in fetal and in adult dolphins. The terminal nerve ganglia contain many large-diameter myelinated fibers and the ganglia are grossly larger than those seen in other mammals.

Two external respiratory openings (blowholes) are present in baleen whales and one in toothed whales. In dolphins, a single blowhole with its muscular plug sits atop a system containing three pairs of asymmetrical sacs below which are paired respiratory passages. Although there are no olfactory nerve endings, the paired external air passages and their associated cartilage, sacs, and muscles are referred to as the nasal system.

5. The gustatory sense

Because the dolphin is regarded as anosmic, and because the animals usually swallow fish and other food whole without mastication, some cetologists have doubted that the animals possess the sense of taste. A presumed gustatory nucleus of the thalamus and the elaboration of the seventh and ninth cranial nerves suggested to neuroanatomists, however, that the gustatory sense is well developed.

Recently, at least three histological studies have produced descriptions of taste buds within five to eight pits that form a V-shaped row on the dolphin tongue. In one study, taste buds were found in the tongue pits of young dolphins, but not in those of adults; in another study, a nerve supply to the buds

could not be demonstrated. There still seems room for doubt that cetaceans have taste buds such as those present in man and most other mammals. Nonetheless, there appears to be psychophysical evidence for chemoreception by sensors in the tongue or mucous membranes of the mouth since, reportedly, trained animals can detect chemicals dissolved in sea water.

6. Asymmetry of the dolphin brain

Toothed whales, but not baleen whales, generally have a strikingly asymmetrical cranium. The blowhole is shifted to the left of the cranial midline, and several skull and head structures on the right are larger than those on the left. There is no known reversal of the family-specific asymmetries among any individual odontocete. Several early authors also reported asymmetries of the brain. These observations have often been discounted because of the possibility that such large brains might be liable to deformation during long periods of fixation.

Recent studies of *Tursiops* and *Delphinus* brains have shown that not only brain size but cortical surface area is also asymmetrical. The right cerebrum is slightly larger. One plausible explanation was given by M.M. Slepsov who argued in 1939 that, in the embryonic state, the left olfactory nerve and lobe degenerate more rapidly than those on the right initiating a series of cerebral and cranial asymmetries.

7. The visual system

The Ganges dolphin with tiny optic nerves and small lensless eyes is almost blind. Some other river species of dolphins also have small, atrophied eyes. Marine cetaceans, however, have well-developed optic nerves and large eyes. In the bottlenose dolphin and the fin whale, rods and cones have been described in the retina. In *Tursiops*, there is no distinct fovea centralis, the retina is thick, and a layer of giant ganglion cells (cell bodies up to 150 μm in diameter) appears to serve most of the central retina. These giant ganglion cells support giant dendrites and myelinated optic nerve fibers that range up to 8 or 9 μm in diameter.

In most mammals, each eye projects the majority of its nerve fibers to the opposite cerebral hemisphere (crossed fibers); however, considerable numbers of uncrossed fibers project to the cerebral hemisphere on the same side. Dolphins, and very likely other cetaceans, are an exception to the general rule that crossed and uncrossed fibers arise from each eye. Three degeneration studies and one physiological study of evoked potentials indicated that each of the bottlenose dolphin's eyes projects only to the contralateral hemisphere. (One study of the harbor porpoise suggests only a 90% crossover.) Total decussation of the optic nerve across the optic chiasm is highly atypical for mammals but common in other vertebrates. It may also be noteworthy that, compared with the human brain, the cetacean brain has a small corpus callosum – only one-quarter as large (Figure 4).

Although the eyes of all cetaceans are widely spaced on either side of the head, it appears that at least *Tursiops* has some degree of visual overlap ventrally and rostrad as well as dorsally and slightly caudad. Despite these small areas of overlap in the visual field, the dolphin's eye movements are not conjugate. The dolphin corneal reflex appears well developed and the pupil reacts to light. The retractor bulbi is large, and the other extrinsic ocular muscles are present and well developed. The oculomotor nerves are small compared with the fifth, seventh, and eighth cranial nerves, but are by no means rudimentary. The presence of an Edinger–Westphal nucleus is questionable. Description of the oculomotor nuclei has been complicated by the presence of a large encapsulated group of cells just dorsal to the third nucleus, the nucleus ellipticus. The function of this

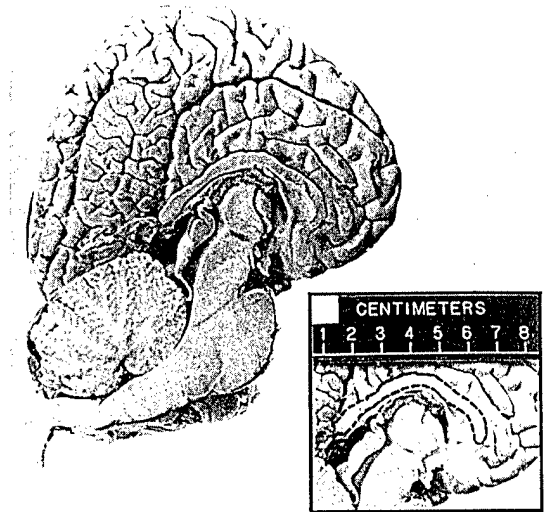


Figure 4. Mid-line view of the brain of an older female bottlenose dolphin (*Tursiops* age about 30) showing the small corpus callosum relative to total brain size.

mesencephalic nucleus ellipticus remains obscure and it has no homolog in other mammals, except for elephants and possibly seals.

The superior colliculus forms an obvious prominence in all cetacean species. In many, such as *Tursiops*, the superior colliculus is only a fraction as large as the inferior (acoustic) colliculus, a reversal of the size relationship seen in humans and other land mammals. The lateral geniculate nucleus is readily identifiable, but, in *Tursiops* and *Delphinus* at least, there is reported to be no true lamination such as occurs in mammals with binocular connections. Mapping studies by Soviet investigators have located visual cortex not at the extreme occipital pole, but in a superior and medial position. The density of calretinin-positive neurons in dolphin visual cortex is low compared to the equivalent area of human cortex.

8. Dolphin sleep

Soviet investigations appear to support an earlier claim by American observer, John Lilly, that dolphins can sleep with one cerebral hemisphere awake. The Soviets reported marked asymmetries in electroencephalograms (EEG) from right and left hemispheres of *Tursiops* and recognized three dolphin sleep stages: stage 1, desynchronization; stage 2, intermediate synchronization including sleep spindles and theta and delta waves; stage 3, maximal synchronization, when delta waves of maximal amplitude occupied not less than 50% of each scoring interval. Stages 1 and 2 occurred bilaterally or unilaterally. Stage 3 occurred in only one hemisphere at a time. Wakefulness or bilateral EEG desynchronization (EEG stage 1 in both hemispheres) occupied 50 to 60% of the recording time. Stage 2, intermediate synchronization, was sometimes recorded bilaterally, and at such times dolphins displayed EEG patterns typical of terrestrial mammals. Unihemispheric slow wave sleep (stage 3 in only one hemisphere), the main type of sleep observed in the dolphin brain, occupied 30 to 40% of recording time and could last more than two hours. Paradoxical or REM sleep was not found in extensive recordings of some 30 dolphins. American workers, however, reported a brief period of REM (based on loss of "trunk" muscle tonus) from a single night's recording of pilot whale EEG.

9. The senses of touch, temperature and pain

The cetacean trunk and tail are normally smooth, firm, and entirely hairless. Mysticetes have bristles or tiny vibrissae about the forward portion of the head. Fetal odontocetes have one or several vibrissae on either side of the snout or upper lip, but these fall out around the time of birth, leaving only whisker pits barely visible in adult animals. On histological section, these pits can be seen to contain the remnants of the vibrissae and a good nerve supply. Encapsulated nerve endings are found in the dermis. These endings are especially numerous about the head, and around the blowhole, anus, and genital slit. The trigeminal nerve, the largest of the cranial nerves in Mysticeti and exceeded only by the auditory nerve in odontocetes, has a prominent ganglion. Trigeminal sensation is better represented than general body somatosensation. The tactile thalamus is reduced compared with that of other mammals. The arcuate division is more developed than the external division, reflecting a greater representation of the face in animals that have relatively large heads.

Mapping studies have located somatosensory cortex in an area postero-lateral to and bordering motor cortex and anterior to and bordering visual and auditory cortex. Skin sensitivity of small odontocetes has been studied with evoked potentials to stimuli such as vibrating, tapping, stroking or dripping water on the skin recorded from contralateral somatosensory cortex. In *Tursiops*, greatest skin sensitivity was on the head – the upper and lower lip near the commissure, around the eyes, and around the blowhole. Stimuli to the body trunk and tail produced minimal evoked potentials. Soviet investigators used the galvanic skin response (GSR) to stimuli produced by a 0.3 mm weighted wire to make a partial map of body skin sensitivity in *Delphinus delphis*. The authors considered their values for the threshold of sensitivity to touch around the dolphin eyes and blowhole to be close to the figures for a human being in the most sensitive skin areas, i.e., the tactile surfaces of the fingers, the skin of the eyelids, and the lips.

No systematic studies have been done on pain perception or sensitivity to temperature. My observations, made largely during the veterinary care of odontocetes, suggest that these cetaceans are sensitive to painful stimuli to roughly the same extent as domestic animals and must be anesthetized for surgical procedures.

10. The auditory system

Hypertrophy of the auditory system may be the primary reason for the dolphin's large brain. The medial geniculate nucleus is about 7 times larger than that of the human, the inferior colliculus is 12 times larger, and the nucleus of the lateral lemniscus is over 250 times larger than in humans. The ventral cochlear nucleus and some other brainstem nuclei also seem massive when compared with the human equivalent. The cetacean auditory nerve has several times as many fibers as the eighth nerve of man. Studies of fiber spectra have revealed larger myelinated fibers in odontocetes than in mysticete whales and the auditory structures are in general larger in odontocete brains. Peak fiber diameters in the sperm whale eighth nerve were about 9 μm , in the bottlenose dolphin about 7 μm and in the fin whale about 5 μm . Auditory tracts reaching the cerebral cortex are extensive. Some observers of the dolphin brain suggested that the cerebral cortex may have reached its great development on the basis of acoustic input.

Mapping the auditory cortex. Soviet investigators located extensive auditory projection areas on the dorsal surface of each hemisphere about 1.5 to 3.0 cm lateral to the sagittal suture. Thus, compared with most land mammals, there is in the dolphin brain an apparent shifting of the auditory area

from the temporal to the parietal lobe and the dorsum of the hemisphere. Evoked potential data suggest the presence of both primary and secondary auditory cortex whereas histological investigation does not. On physiological grounds, the bat also exhibits complex organization of the auditory cortex, yet, like the dolphin, shows the histologist a more primitive level of cortical development than, for example, carnivores or primates. The extent of auditory cortex in dolphins may be greater than that indicated in the mapping experiments previously mentioned. A tonotopic map of the cochlear projections on the dolphin cortex has not been done; nor have complex stimuli of different delays or rise times or other acoustic characteristics been used in attempts to find areas of cortex specialized for specific information bearing parameters like those found in bat cortex. Therefore, it is entirely possible that further auditory projection areas will be found in temporal cortex, which, in the dolphin, is less accessible than the dorsal area that has been mapped.

Hearing and the ear. The mammalian ear evolved for hearing in air. In assuming the aquatic mode, the cetaceans have modified this aerial system, and audition has apparently become their most highly developed sense. When the distant ancestors of the cetaceans entered the aquatic medium with their aerial ear, it is almost certain that they could immediately hear high frequency sounds conducted directly through the body because body tissues are well matched with water for sound conduction. Human divers can hear high frequencies underwater, but, because of the upper frequency limit of human hearing, there is no pitch discrimination in the ultrasonic region above about 20 kHz. The evolution of the dolphin ear has apparently been a process of enhancing those characteristics that allowed for greater high-frequency hearing sensitivity and complex auditory processing. Audiograms have been done on several species of smaller odontocetes by both behavioral and electrophysiological techniques. *Tursiops* responds to frequencies as high as 150 kHz with greatest sensitivity between about 20 and 100 kHz – their hearing at frequencies below 1 kHz is relatively poor.

Although no auditory studies have been done on the large baleen whales such as the blue and fin it is assumed that their hearing sensitivity may be shifted to the low frequencies since they produce calls as low as 16 to 20 Hz.

All cetaceans lack a pinna and the external auditory meatus has apparently become a vestige in most species. The dolphin ossicular chain is stiff and the malleus does not attach directly to the tympanic membrane. In modern dolphins, the basilar membrane of the cochlea is relatively long (35 to 40 mm in *Tursiops*) and very narrow near the basal end (25 μm in *Tursiops*). The number of inner hair cells in the dolphin cochlea is about the same as, and the number of outer hair cells only slightly greater than, in humans, but the number of ganglion cells is much larger. The ratio of ganglion cells to hair cells (inner and outer) is roughly 2:1 in humans and 5:1 in *Tursiops*.

Echolocation. Research on dolphin echolocation done during the past thirty years has confirmed an earlier suspicion. Men who collected the first permanent captive dolphin colony at Marine Studios in Florida in the late 1930's and 1940's suspected that dolphins possessed some sort of sonar or echolocation ability. Studies have since shown that blindfolded *Tursiops* can make extremely fine discriminations over underwater ranges of at least 100 m by employing trains of high-frequency clicks emitted from the nasal system and directed forward in a fairly narrow beam.

Electrophysiological experiments with dolphins have shown that temporal resolution of successive sounds is extremely rapid and that very small changes in stimulus frequency altered evoked potential (EP) amplitude and waveform. The typical midbrain EP of *Tursiops* appears specialized for ultrasonic, ultrabrief, fast-rising, closely-spaced sounds like the echoloca-

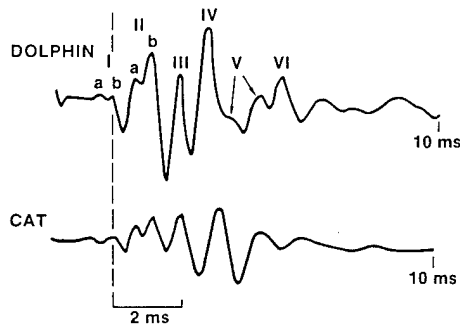


Figure 5. Click-evoked dolphin (*Tursiops*) averaged brainstem response compared with that of the cat. The great hypertrophy of the auditory brainstem and large auditory fibers gives rise to a robust ABR with waves of relatively short latency, even when compared to much smaller-brained species.

tion clicks. However, at several cerebral locations (mainly in the posterior lateral temporal cortex) long latency, long duration, slowly recovering EP's have been evoked by lower frequencies, with either fast or slowly rising acoustic envelopes. This suggests dual analysis systems, one specialized for the ultrasonic click and the other for lower frequency sounds such as whistles and squeals produced by many of the smaller odontocetes and some other whales as well.

The averaged brainstem response (ABR) can be recorded from electrodes on the skin surface or placed subcutaneously over the dolphin cranium. The click-evoked dolphin ABR consists of 7 waves within 10 msec, numbered by the positive peaks at the vertex (Figure 5) and corresponding well in respect to latency of each peak with waves in other mammals. The dolphin ABR waves are large, sometimes reaching an amplitude of 10 μ V. The waves decrease in amplitude and increase in latency as click stimuli are attenuated. The latency-intensity function is flat compared with that of other species. Brain stem transmission time (BTT) is considerably faster in *Tursiops* (brain weight around 1500 g) than in humans or domestic cats and is similar to that of the rat. Despite a much longer nerve pathway, BTT in the dolphin is equal to or faster than that in much smaller brained species. It has been suggested that, due to larger auditory myelinated fiber diameters, the axonal conduction velocity is higher by just enough to compensate for a longer path in the dolphin brainstem.

11. The facial nerve

The main facial nucleus lateral to the superior olive is large and conspicuous. The dolphin facial nerve is well developed and apparently supplies the extensive musculature of the blowhole, nares and nasal sac system. Since sound production is so important to animals that use echolocation and rely upon sound for underwater communication, such development is not surprising.

12. The spinal cord

The spinal cord is nearly cylindrical throughout. A cervical swelling is present in all species studied, but the lumbar enlargement is described as absent or not prominent. The fin whale and harbor porpoise have 44 spinal nerves – eight cervical, 12 thoracic, and 24 lumbocaudal. The anterior horns are long and slender, occupying about one-half of the grey matter. The posterior horns have a stunted appearance. A short, pointed lateral horn is discernible at thoracolumbar levels. In *Tursiops*, the ventral columns of white matter are strongly developed. Clarke's columns are fused into a single median

nucleus, at least in the caudal part. The pyramidal tract is very small. The cortical projection into the cord is rather small; however, there seems no doubt that corticospinal fibers are present and form a crossed projection in cetaceans. According to one observer, the morphology of muscle spindles and neuromuscular junctions in *Tursiops* appeared similar to those of other mammals.

13. The pineal, mammillary bodies, and pituitary

In numerous dissections, I have never found the pineal body which is considered absent by most observers of the odontocete brain. There is one report of a small pineal from a mysticete, the humpback whale. The organ is also present in embryonic stages of the blue whale. Gross examination does not reveal mammillary bodies, but mammillary nuclei are recognized histologically. The pituitary is well developed with adenohypophysis and neurohypophysis separated by a dural septum.

14. The cerebellum

In the embryonic stage, the dolphin cerebrum and cerebellum are about equal in width. According to paleontologists, the earliest cetaceans were the first giant mammals adapted to life-long swimming. These ancient cetaceans already had a large cerebellum that was wider than the cerebrum. In modern odontocetes, the cerebrum has so enlarged as to cover the anterior portion of the cerebellum. In baleen whales, the cerebellum may be more than 20% of total brain weight; in dolphins, the cerebellum comprises about 15% of total brain weight, compared with the 10% of humans, cats and many other mammals including some of the primitive river dolphins, the sperm whale, and pygmy sperm whales. The cerebellum of the largest baleen whales, without digits, and presumably without fine movements, is huge, ~1,500 grams.

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See also Brain asymmetry, animal; Brain size; Echolocation; Evolution of vertebrate brains; Neuroscience, comparative; Auditory system

Chaos in brain function

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The possibility that chaos might represent meaningful information in brain function may seem a bit strange at first thought because, as the name seems to imply, how could something chaotic represent the encoded or stored information for something specific? It is necessary, therefore, to address the issue of the definition of chaos itself.

In mathematics the term chaos refers to orderly processes that generate complicated, often random looking activity, from simple, nonrandom mechanisms. That is, chaotic processes are fully deterministic, yet fulfill most of the statistical criteria for randomness. In anticipation of the following discussion, we may say that chaotic processes are short-term but not long-term predictable. As an introduction to the neurobiology, this discussion will examine two sets of mathematical equations that generate chaos, the logistic and Rössler equations. Then, after examining some of the evidence and problems associated with the demonstration of chaos in biological systems, the discussion returns to the above question on information storage.

1. Logistic dynamics

Recursion and bifurcation. Recursion is a process whose future position occurs through feedback to its previous position. The logistic equation, $X_{n+1}R(1 - X_n)X_n$, provides an example of recursion. The new value, X_{n+1} , is generated through the previous value X_n . The new value is fed back to the right side of the equation to generate another value on the left side. For values of X_n between 0 and 1, the generation of new values is predictable for R ranging between 0 and about 3.5, whereas for R ranging between 3.5 and 4, the sequence of numbers appears complicated and is not long-term predictable. On the right side of the equation, $X_n \times X_n$ provides the nonlinear drive. R is a parameter that controls the ability of the system to express different activities. Bifurcation is the process by which new response forms appear as a function of the controlling parameters, and, therefore, these constants are called bifurcation parameters.

The controlling effect of R is shown diagrammatically in Figure 1. To generate this illustration, the value of R was systematically altered by small steps between 0 and 4. With each value of R , the equation was recursively iterated for an arbitrarily selected number of steps (R steps of 0.001 and 200 iterations for each step give reasonably good resolution). For each R less than 3, all iterations yield the same X_{n+1} series of values. If one were to think of action potentials (spikes) in neurons, the equivalent observation would be of a series of spikes separated by equal intervals. Therefore, all 200 X_{n+1} values fall exactly at one point in Figure 1. The upward sloping line in Figure 1 between 0 and 3 shows that X_{n+1} increases with R . In neuronal terms, one would expect to see a lengthening of the interspike interval as R increases.

For R a little larger than 3, X_{n+1} bifurcates into two new values. For neurophysiologists who are accustomed to listening to action potentials on audio monitors, one would hear a transition from a one-cycle sound (bop, bop, bop, bop) to a two-cycle (bop-bop, bop-bop). As R increases, the intra-bop-bop interval becomes shorter, whereas the interval between successive bop-bops becomes longer. At larger R , the sequence of X_{n+1} values bifurcates into four-cycles, then eight-cycles, and finally, at about $R = 3.6$ into two-cycle chaos. Thereafter, for a broad range of R , the logistic generates broad-spectrum chaos, all of which are much more complicated than the simple bop-bop. We shall get back to the reasons why the chaotic regions are actually chaotic, but take it on faith for the moment that the scatter of the 200 points in the vertical axis is chaotic, and that none of the points overlap one another, even though the pixels in the computer-generated graphics of the illustration do overlap. Expansion of the R -axis, say between 3.900 and 3.901, and reduction of the R -steps to 0.0001 to give better resolution, would show that regions along the R -axis contain aperiodic or chaotic data that run into regions of periodicity and then back into chaos; periodicity means that the same values are generated from one iteration to another. For purposes of illustration, the remainder of this discussion examines the logistic values generated when $R = 3.95$.

Time series. When plotted as a time series, the sequence of points in the 3.95 logistic seem irregularly or randomly scattered. This is shown in Figure 2A (The lines connecting the points should not be shown because initiating the equation using different values for the first X_n , would not have produced points lying between the ones shown here, but rather an entirely different data set would have been produced. Thus the purpose of the connecting lines in Figure 2A is only to highlight the unpredictable flow of data).

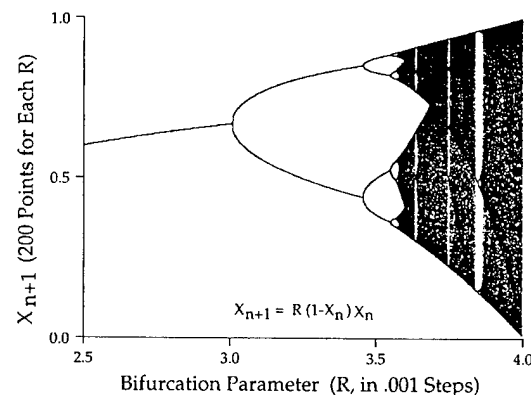


Figure 1. Bifurcation diagram of the logistic equation.