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Title of Study: PHYSIOLOGICAL ADAPTATIONS IN DIVING VERTEBRATES

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Candidate for Degree of Master of Science

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Scope and Method of Study: A review of the literature concerned with physiological adaptations in diving vertebrates was made. The result is intended to serve as a summation of the work done in this area.

Findings and Conclusions: Diving vertebrates show some adaptations to the threat of asphyxia due to prolonged dives. The most universal adaptation is bradycardia or slowing down of the heart rate. This has been shown to occur in nearly all diving animals studied, and also in some non-diving animals. Along with the bradycardia, vasoconstriction is also found. The muscles, kidneys, intestines, and other areas show the constriction. The heart and brain, which have very little tolerance for anoxia, during this time has normal or even increased blood flow. Reduction of metabolic rate in the peripheral tissues is another adaptation found in the diving vertebrates. The results of the adaptation is to reduce the diving animal to a heart-brain-lung preparation. The effect is to provide the tissues that are not tolerant to asphyxia - the heart and brain - with the most optimum environment possible under diving conditions.

Some other adaptations found in other diving vertebrates are also reviewed in the manuscript.

ADVISER'S APPROVAL

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PHYSIOLOGICAL ADAPTATIONS IN
DIVING VERTEBRATES

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PHYSIOLOGICAL ADAPTATIONS IN
DIVING VERTEBRATES

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Some other adaptations found in other diving vertebrates are also reviewed in the manuscript.

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PREFACE

This paper is intended to serve as a review of the work that has been done in the area of physiological adaptations in the diving vertebrates.

I wish to acknowledge and thank Dr. L. Herbert Bruneau for the time required of him in helping and guiding me in the preparation of this manuscript and would also like to thank Mrs. Sharen Van Zandt for her patience in the correcting of errors and her typing of the final copy.

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CHAPTER I

INTRODUCTION

Man has for many years been interested in the sea. It has presented a challenge that has been difficult to pursue due to the fact that man is a terrestrial, air-breathing animal. One area of interest to man has been the natural divers. Why certain closely related animals are able to survive the threat of asphyxia so much better than their terrestrial relatives is a question that may be answered. Since Bert in 1870 first found that avian divers exhibited bradycardia, the study of the natural diving animals has been pursued. Bert, Richet, Scholander, Elsner, Andersen, Johansen, Ommanney, and Irving are a few of the noted scientists who have done or are doing work in this area.

What is the point in studying diving animals? One answer is that these animals display to an extreme degree the ability to cope with a stress which in one form or another is common to man, namely, acute asphyxia. Perhaps in the study of these animals information may be uncovered which will be useful in solving some of the problems of man.

The purpose of this paper is to present some of the information that has been brought out by various scientists. Some of the information is similar but has been done on different diving animals, or has been done under different conditions. The reader should find the information of interest.

CHAPTER II

THE MORE UNIVERSAL ADAPTATIONS IN DIVING VERTEBRATES

The land vertebrates are equipped with special organs serving respiration, the lungs, the large surfaces of which are contained in cavities within the body. Gas exchange with the environment is accomplished by a continuous and rhythmic ventilation of the respiratory organs. A number of mechanisms, such as a carbon dioxide sensitive respiratory centre, chemoreceptors that detect changes in the tensions of carbon dioxide and oxygen in the arterial blood, and pulmonary stretch receptors, ensure that the rate of ventilation is adjusted to the requirements of the organism. Thus, the maintenance of homeostasis with respect to the blood gases is carefully safeguarded in the organism. In man, and probably in all homeothermic animals, breath-holding soon evokes unpleasant sensations. The asphyxiation which results becomes acute in a few minutes, and continued respiratory arrest is very rapidly fatal. There is, however, one group of vertebrates that has developed a striking ability to cope with acute asphyxia, namely, the natural divers.

Most body parts have tolerance to asphyxia; the arm, leg, kidney, and others. However, the heart and brain are irreversibly damaged by asphyxia and are extremely sensitive to lack of oxygen. How then are animals such as ducks able to stay submerged from 10 to 20 minutes, and seals for 20 minutes or more, and whales for an hour or two? Oxygen binding pigments such as hemoglobin in the blood and myoglobin in the

muscles, along with lung storage are not the answer (Scholander, 1963).

The respiratory and circulatory organs of diving reptiles, birds, and mammals do not differ in functional respects from those of their terrestrial relatives. There are, therefore, a number of possible explanations for the ability of diving vertebrates to endure prolonged submersion.

Two possible explanations for the ability of diving vertebrates to endure prolonged submersion are: (1) Oxygen stores may be extraordinarily large so that they permit normal consumption of oxygen during diving, and are refilled upon emersion. (2) Physiological adaptations may take place during submersion, thereby, securing an adequate supply of oxygen to the tissues especially sensitive to oxygen deficiency, the heart and the brain, whereas those tissues more resistant to transient anaerobiosis are left to manage through the period of submersion practically without oxygen (Andersen, 1964).

Bert, in 1870, started the inquiry as to why diving animals have the ability to ward off asphyxia. It was thought by him that because the blood volume of a duck was larger than that of a chicken, the oxygen content of the duck was the answer for the prolonged stay under water. Richet in 1894 showed that even though the duck had more blood, there was not sufficient difference to allow for the offset of asphyxia, considering the time involved. (See Table I). In 1899, Richet stated the difference was due to oxygen sparing mechanisms (Andersen, 1964).

The oxygen stores of diving vertebrates are from three main sources: (1) lung air. (2) blood. (3) muscles. If these are considered as explanations for the prolonged diving ability, the following facts must become apparent. Seals are known to dive on expiration and

TABLE I
 DURATION OF SUBMERSION BY DIVING AND NON-DIVING VERTEBRATES
 (Andersen, 1964)

Animal	Time (Minutes)	Reference
Alligator	120	Andersen (1961)
Pigeon**	1	Bohr (1897)
Hen**	3	Bohr (1897)
Guillemot**	12	Bohr (1897)
Penquin	7	Scholander (1940)
Duck	15	Andersen (1959 a,b)
White rat**	2	Bert (1870)
Rabbit**	3	Bert (1870)
Cat**	3	Bert (1870)
Dog**	4	Bert (1870)
Muskrat**	12	Irving (1939)
Beaver**	15	Irving (1939)
Grey seal	18	Scholander (1940)
Bladdernose	18	Scholander (1940)
Fin Whale	30	Scholander (1940)
Bottlenose	120	Scholander (1940)
Man	1½	Scholander <u>et al</u> (1962)

** Average time to last movement by forced submersion

therefore, would have little or no lung air available. Reptiles and birds exhale large quantities of air prior to or during submersion, again showing little available lung air. If air is kept in the lungs, it may cause caisson disease and may also affect the buoyancy of the animal. The blood volume of the divers is only approximately twice that of the non-divers, however, the oxygen capacity of the blood is greater in the natural divers, but this would extend the diving times only three to five minutes over the non-divers. Aquatic mammals have dark muscles, that indicate a high content of myoglobin. The myoglobin content of seal muscles was determined by Robinson, who found that 47% of the total amount of oxygen available during submersion may be stored in the tissue. This, he thought, might provide oxygen for the brain and the heart. Hemoglobin gives oxygen to the myoglobin, however. Therefore, the myoglobin would not provide oxygen to the sensitive parts. Birds and reptiles have muscles lighter than the mammals thereby containing less myoglobin (Andersen, 1964). These things would indicate that oxygen supply alone would not allow for the same rate of use by these animals while submerged.

In 1870, Bert observed that a bradycardia or slowing down of the heart rate took place in submerged ducks (Andersen, 1964). Scholander in 1940 said bradycardia of 5% to 10% of normal cardiac rhythm is observed in diving reptiles, birds, and mammals, with the exception of the whales. It occurred in every animal studied, such as seal, porpoise, hippopotamus, dugong, beaver, duck, penquin, auk, crocodile, and turtles. Fishes out of water even show bradycardia. Non-divers also show bradycardia but it is much less pronounced (Scholander, 1963). In whales a special anatomical arrangement of arterio-venous shunts

seems to make the usual circulatory adjustments to diving unnecessary. Bradycardia develops differently among various divers. In the seal, it develops immediately.

Robert W. Elsner trained seals to dive by submerging their nose in a basin of water. Scholander secured the seal to a board and submerged the seal's nose. Within a very short time after the seal's nose submerged, the heartbeat dropped to approximately one-tenth of normal. The fact that the slowing down occurs quickly shows that this is a reflex action and is not brought about by metabolic change. Sometimes bradycardia fails to show if the animal knows it is free to raise its head and breathe. On long dives it is always pronounced even with hard work being done by the subject. Bradycardia can even be triggered when the seal is completely out of water by all sorts of sudden stimuli, auditory, visual, or tactile. In most animals, however, bradycardia develops gradually (Scholander, 1962).

In the sea lion the heart rate dropped from 130 beats per minute to 40 beats per minute beginning approximately ten seconds after the nose was submerged. Cardiac output decreased proportionally (Elsner, 1963). In diving snakes bradycardia developed within two minutes in all cases (Murdaugh, 1962). In ducks the heart rate of 250 to 200 beats per minute dropped to less than 40 beats per minute. In one example pre-immersion frequency was recorded at 210 beats per minute, bradycardia developed gradually and did not become conspicuous until about 25 seconds after immersion. After 45 seconds the heart beat had dropped to 20 beats per minute (Johnsen, 1963). Hollenberg (1963) states,

The fall in heart rate was generally apparent within seconds, moderate within 15 seconds, and progressed to a maximum fall by about 60 seconds and was so maintained until the end of

the period of submersion, interrupted only by brief bursts of tachycardia during a struggle.

In studies on the American alligator, the pre-dive heart beat was 41 beats per minute. In an involuntary dive the rate would increase when first submerged, but within 10 minutes would drop to 2 to 3 beats per minute. In voluntary dives the rate was 24 beats per minute and would drop to 30% to 50% of the pre-dive rate (Andersen, 1963).

The reduction of heart rate must have some effect on the animal. It must be realized that bradycardia cannot be an isolated adjustment. Other changes must compensate for or be compensated by such a pronounced decrease in heart rate. Recordings of the blood pressure during diving indicates that pronounced vasoconstriction accompanied by an increase in the peripheral resistance takes place during submersion. Central blood pressure stays at a normal level during the time of reduced heart beat. Pressure traces show the pressure rise with each heart beat to be normal, but the subsequent drop in pressure is gradual and prolonged. This shows the systolic phase as normal but the diastolic phase during which the blood is forced through the aorta, encounters resistance. The peripheral blood vessels are constricted. Measurements in a small toe artery in a seal's flipper show pressure drops at the start of a dive, falling rapidly to the level maintained in the veins. The flow is shut down to practically nothing. Irving in 1934 noted that Gesell's discovery in 1927, that a dog rendered asphyxiated by excess carbon dioxide and lack of oxygen showed muscle circulation slowed down at normal pressure and brain circulation increased, might explain a diving animal's resistance to asphyxia. He measured blood flow with heated wire probes and recorded the rate at which heat was dissipated. He confirmed the fact that the blood flow in the muscles was reduced,

but brain flow remained constant or increased. He decided the defense would prove to be some mechanism for selective redistribution of the circulation, with preferential delivery of the decreasing oxygen store to those organs that can least endure anoxia: the brain and the heart (Scholander, 1963). Other investigators confirmed the fact of vasoconstriction. A wound may bleed while the animal is breathing air but upon submersion the bleeding stops, but continues again after emersion. Myoglobin in the muscles may be completely reduced while arterial blood is still half-saturated with oxygen (Andersen, 1964). Cessation of renal function during diving was shown by Murdaugh (1961). It was found that urine flow stopped within one minute of the time the head of a seal was submerged. No urine was formed during the remainder of a 10 minute diving period, but urine flow returned within 2 minutes of the end of submersion. The absence of urine production appears to be caused by a cessation of glomerular filtration and not by an increase in tubular reabsorption of water (Murdaugh, 1961). Blood flow in submerged ducks dropped to 3.9% in the gizzard, 29.4% in the skin excised from the thorax, 11% for gastrointestinal muscle, and 9.1% in the kidney. Muscle and skin from the head region increased flow, as did the eye and esophagus. The myocardium from both atria and ventricles showed a striking increase amounting to 4.1 times higher activity as did the adrenals which showed 4.9 times normal blood flow (see table II) (Johansen, 1964b).

Another factor that reinforces the vasoconstriction evidence is the lactic acid levels. Lactic acid is the end product of the anaerobic metabolic process from which muscles derive energy in the absence of oxygen. The concentration of lactic acid in the muscle tissue rises

TABLE II
CHANGES IN ORGAN ACTIVITY

Table demonstrates changes in organ activity comparing normally breathing (N) and submerged (S) animals as counts per gram tissue per minute. The heart rates are indicated at the bottom of each column. The table has been modified to give the average of the original table. (Johansen, 1964b).

TISSUE	N	S	%
Skin			
Web	246	185	-
Thorax	3745	1089	29.4
Head	3990	13065	237
Muscle			
Gastrocnemius	5571	618	11.0
Pectoralis	5782	1364	23.6
Neck muscle	3143	1103	35.9
Masseter	2640	5875	222
Heart			
Left atrium	7957	46967	565
Right ventricle	14570	68287	468
Left ventricle	29842	113486	407
Gastro-intest			
Esophagus	2449	8044	320
Gizzard	4619	254	3.9
Intestine	9558	2005	20.9

TABLE II (Continued)

Tissue	N	S	%
Glands			
Pancreas	7060	554	7.8
Liver	7612	6116	80.3
Adrenals	3415	8494	497
Throid	3454	8494	245
Kidney	61083	5560	9.1
Spleen	7175	6573	91.6
Eye	4374	16676	381
Diencephalon	535	1747	326
Heart rate (beats/min.)	190	15	7.9

sharply during diving, but the concentration in the blood does not. When the animal starts to breathe again, lactic acid floods into the bloodstream. The blood is flushed with 3 to 10 times the amount of lactic acid as when at rest. As an example, in the duck the concentration of lactic acid in the blood rises relatively slowly during diving compared to the steep increase seen upon emergence. In the experiment the lactate level rose from a prediving value of 2.0 to 5.1 mM/l. after 13 minutes of submergence. During the initial two minutes of the recovery period an additional increase of 8.5 mM/l. was observed. This shows the muscle circulation remains closed during the dive. The oxygen disappears from the muscle tissue a few minutes after the animal submerges, but the arterial blood still has plenty of oxygen. All of this evidence shows the peripheral circulation shuts down and is evidently the reason that the heart slows down (Scholander, 1963). The success of the divers depends partially upon their ability to turn in to a heart-lung-brain preparation upon submersion. They undertake to convert themselves into a much smaller animal as far as oxygen supply is concerned.

The temperature of diving animals drops at the extremities during a dive more rapidly than in the interior. Upon emersion all parts of the body has a drop in temperature, the abdomen most of all. Rapid blood flow upon emersion takes heat from the central area to all parts, thereby, dropping the central temperature (Andersen, 1964). During these dives what happens to energy metabolism?

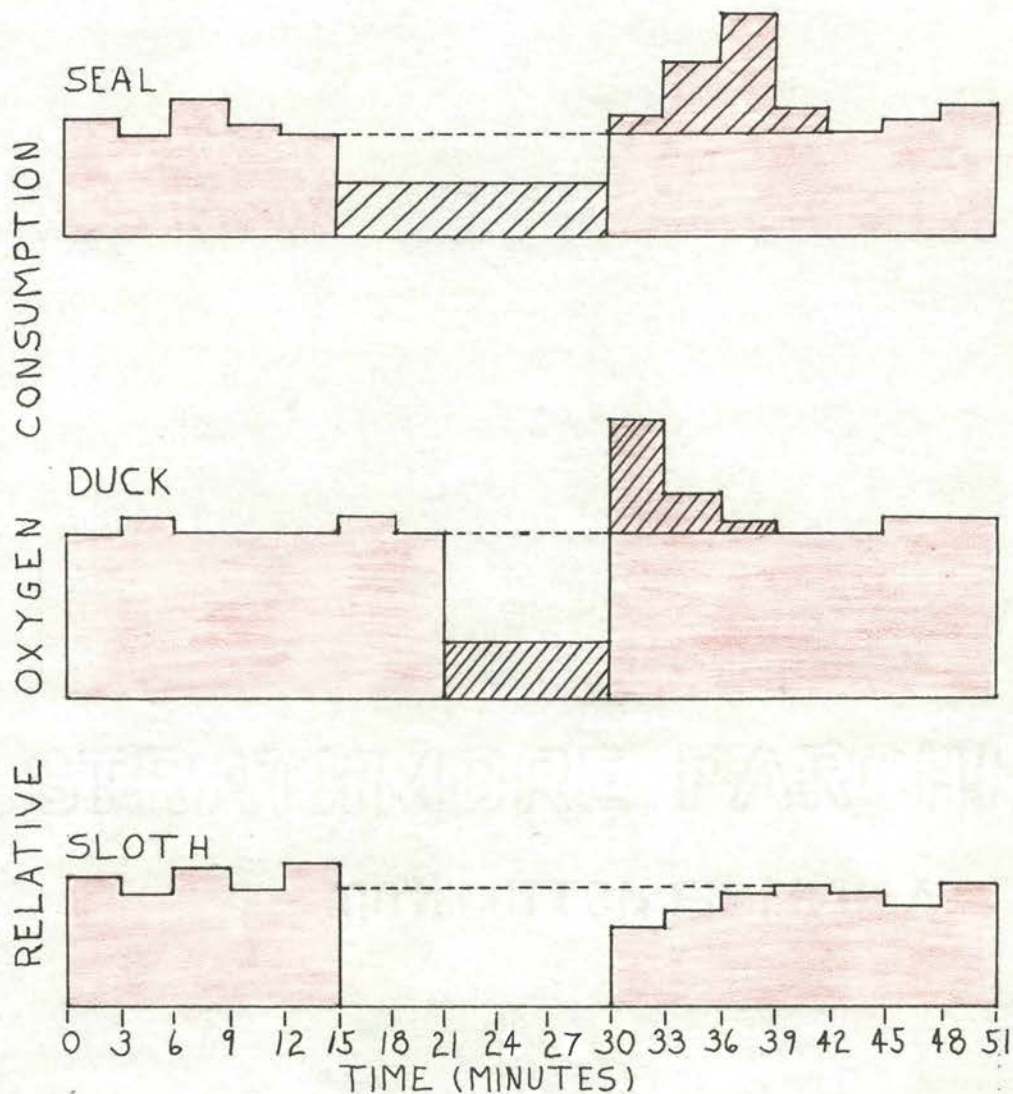
When the oxygen capacity of a diving animal is compared with the metabolic rate at rest and the maximal diving time that is endured under experimental conditions, it appears that the oxygen stored within

the organism is not sufficient for an aerobic metabolism even at the resting rate during a prolonged dive. Richet suggested that the metabolic rate is very much lowered during a dive. The hypothesis of a diminished diving metabolism has strongly been supported during the last 25 years through the studies of metabolic rate by indirect and direct calorimetry and by measurements of body temperature. This could be a general lowering of the metabolic rate or a few organs may maintain the metabolic rate whereas cellular combustion elsewhere became extremely low. It is most likely accomplished by a series of suitable cardiovascular adjustments which allow a selective use of available oxygen governed by a differential distribution of the blood, thereby, reserving the oxygen for the central nervous system and the heart (Andersen, 1964).

Metabolism is best studied during a quiet dive by a trained seal or duck. The oxygen stores are large enough to provide only a quarter of the energy expended in a predive resting period of the same length. Do anaerobic processes including lactic acid production substitute fully for the lack of oxygen? Oxygen debt that incurs must be paid off when oxygen becomes available. Excess oxygen intake on recovery from a dive is a measure of the debt. If energy rate during the dive was the same as before the dive, excess intake would equal the normal oxygen-consumption rate during the dive. It was found for the seal and the duck that it was much smaller, however. The sloth, which is not a diving animal but that shows great tolerance for asphyxia, incurred no debt at all. (see table III). This implies metabolism must slow down. Oxygen studies are not enough. Temperature measurements confirmed the impression of decreased metabolism. It was noticed after long dives,

TABLE III
OXYGEN CONSUMPTION RECORD

Metabolic slowing down during a dive is demonstrated in three animals by the record of oxygen consumption in successive three-minute periods. In the seal and duck the amount of excess oxygen intake after the dive (hatching on color) represents the oxygen debt incurred by anaerobic metabolism during the dive. This debt (hatching on white) is clearly not enough to have sustained an energy expenditure at a normal rate (broken line) during the dive. The sloth seems to incur no oxygen debt while diving (Scholander, 1963).



of 20 minutes or so, that seals would be shivering during the recovery period. Also it was noticed that ducks would fluff out their feathers, a heat conserving mechanism. The animals lost body temperature at a rapid rate while submerged. This was evidently not due to heat loss because there was no substantial change in thermal contact as only the nostrils or beak was submerged. Also, the reduction in circulation meant that heat conductivity was lessened. Loss therefore meant a decrease of heat production- a slowing down of metabolism. Apparently the lack of blood in the tissues jams normal metabolic processes by mass action. Under normal diving conditions, general metabolic slowing down is masked. Food gathering causes exercise expending much energy and muscles depend on anaerobic processes resulting in lactic acid formation. Oxygen debt in such cases makes it impossible to detect the subtle lowering of metabolism that must still occur in the non-active tissues deprived of circulation (Scholander, 1963). What causes these adaptations in the diving vertebrates?

It seems reasonable to assume that the physiological adjustments to diving are elicited, either by the asphyxiation which progressively increases during a prolonged submersion, or by the actual water immersion. Diving bradycardia was found to result in at least three factors:

- (1) A specific nervous reflex resulting from submersion of the head.

This first factor is the permissive and necessary factor for establishing the "diving reflex", but is strongly reinforced by at least two other mechanisms.

- (2) The progressive hypercapnia during asphyxiation.
- (3) The increasing anoxia during the asphyxia (Feigl, 1963).

By using a duck and submerging the head, starting at the tip of the beak and proceeding caudally, one might determine the exact level

of water immersion necessary to induce the physiological adjustments to diving. By reversing the procedure, one ought to be able to establish at which level of emersion of the head the diving characteristics are abolished. The heart rate started slowing down as soon as the rostral end of the beak made contact with the surface of the water. The rate of cardiac slowing decreased or stopped completely as long as the water level did not reach the nares. The main drop in cardiac rhythm occurred when the nostrils and subsequently the whole beak was immersed into the water, and the diving bradycardia was finally somewhat extra accentuated when the whole head became submerged. The heart rate rose slightly when the head emerged so that only the beak remained under water, and when the nostrils were brought up above the water surface, the heart rate increased further. The most important zone by far, for the elicitation of the physiological adjustments to diving, seems to be the caudal part of the beak measured from the rostral border of the nares (Andersen, 1963b).

In snakes bradycardia did not appear until the snake had exhaled. In snakes with obstructed nares no bradycardia appeared. This suggests that as long as water does not enter the nares, bradycardia doesn't occur. When water enters the nares a vagal stimulus occurs with bradycardia resulting (Murdaugh, 1962).

In all essentials the responses of the cardiac rhythm to water immersion of the head were found to be the same in ducks when experiments were performed with animals before and after decerebration. Ducks with intact central nervous systems, but with various deficits in the trigeminal innervation to the beak and the nasal cavity were also studied. When the mandibular, maxillary, and ophthalmic supply

to this region had been completely severed, the usual responses to diving would, as a rule, not be elicited upon immersion of the head into water, regardless of whether the duck could see or not. Sectioning of the maxillary alone did not alter the diving response. When the nerve supply of ophthalmic and mandibular origin had been severed, leaving the maxillaries intact, the duck did not display diving reactions. If only mandibular nerves were cut, it was sometimes possible to immerse into water the part of the beak rostral to the nares without any change in respiration or heart rate. If nostrils submerged, however, diving characteristics appeared immediately.

From this data it may be concluded that the circulatory responses to diving as well as the respiratory responses are independent of levels of the central nervous system higher than the medulla. Our knowledge of the diving characteristics have been extended to include the afferent limb of the reflex arc, however. The latter may be summarized as follows: sensory receptors → trigeminal nerve → medullary centers → vagus nerve (Andersen, 1963a).

Diving animals may be less sensitive to hypercapnia than their terrestrial relatives. Seals show a depressed ventilatory response to carbon dioxide, presumably an adaptive mechanism permitting prolonged diving (Robin, 1964). It is interesting to note that even if passive mechanical stretching of the lungs and air sacs is provided, there is very little effect on the heart rate during diving (Andersen, 1963c).

Besides reserving the oxygen stores for the brain and the heart, another principle required for the safe extension of under-water exposure would be the ability to utilize the oxygen stores to a very

high degree and still maintain a state of useful consciousness. Useful consciousness has been defined to mean that state in which the individual remains attentive and is able to perform useful or purposeful acts (Andersen, 1961). Oxygen in the lung air is used very rapidly at first during a dive, 2/3 of the oxygen being used in the first 1/3 of the dive. It slows to only 3% to 4% of the prediving rate thereafter in the duck. In alligators it slows to 3% to 6% of the prediving consumption. Toward the end of a maximal dive a duck's lung air contains only 3 volume per cent oxygen. An alligator has only 1.5 volume per cent oxygen in the lung air. Before the dive the animals have 17% to 19% oxygen. Man loses consciousness at 8 volume per cent at sea level (Andersen, 1964). Post dive recovery is marked by tachycardia and vasoconstriction (Van Citters, 1965).

CHAPTER III

INDIVIDUAL ADAPTATIONS IN DIVING VERTEBRATES

Some turtles do not show the usual bradycardia and vasoconstriction. The freshwater turtles, Pseudemys scripta, P. elegans, and P. floridana, are able to dive for extended periods in the absence of molecular oxygen. The fundamental adaptation which permits this is the animals' ability to exist for prolonged periods on energy derived solely from anaerobic glycolysis.

The heart of the turtle has four chambers. As has been reported for all reptiles, except Crocodilia, the intraventricular septum between the right and left ventricle is incomplete. The right and left ventricles have a potential communication through this large ventricular septal defect located in the anterior part of the intraventricular septum. At the base of the pulmonary conus is a valve-like cartilaginous structure not previously described. When this structure approximates the septal defect, then the two ventricles are anatomically discrete. When this structure is pulled away from the septal defect, then free mixing of right and left ventricular blood is possible. The origin of each main stem pulmonary artery is invested in a cartilaginous-smooth muscle coat. In ambient air there is some shunting of blood from the left to the right ventricle through the defect. During prolonged diving the shunt is reversed and blood from the tissues bypasses the lung and enters the aorta directly. In the case of turtle

brain, anaerobic glycolysis is capable of maintaining integrity for long periods. Thus, there is no particular necessity for preserving oxygen supply to the brain. Continued blood supply to the tissues serves the purpose of transporting substrate for anaerobic glycolysis. However, when oxygen is no longer available in the lung there would appear to be no advantage in continuing the pulmonary circulation. Studies demonstrate that, indeed, under these circumstances blood is shunted away from the lung and that pulmonary circulation ceases.

The stimulus for the development of the right to left intracardiac shunt appears to be a function of blood or tissue oxygen tension. The exact mechanics which produce the right to left shunt are not clear. Presumably, the development of the shunt is associated with increasing resistance to flow through the pulmonary artery. Whether the unusual cartilaginous-smooth muscle structures located at the origin of the main stem pulmonary arteries participate in the increasing pulmonary vascular resistance is not known.

It is also not clear how the valve-like structure located close to the ventricular septal defect specifically operates to permit free flow of blood from the right ventricle into the aorta. However, the development of a right to left shunt during diving in the turtle is a clear example of a circulatory adaptation which ensures provision of the optimum requirements necessary for metabolism (Millen, 1964).

Another example states the following information. It is concluded that the basis of survival of anoxic turtles is the energy yield of anaerobic glycolysis. Turtles confined to aerated water survived on an average of 59.7 hours, while others confined under anoxic water survived for an average of only 12.7 hours. It is

concluded that aquatic respiration is important to the Loggerhead Musk Turtle, Sternotherus minor, in enduring long periods of submergence (Belkin, 1962).

It has long been a recognized fact that whales can dive much longer and much deeper than other diving pulmonate animals. The sperm whale and the bottle-nosed whale, especially, are known to endure most prolonged and deepest submergence. It is very interesting that the sperm whale and the bottle-nosed whale, both being the champions of all pulmonate divers, possess within their body a large quantity of wax, instead of the usual fat. Moreover, the sperm whale has an enormous special organ, spermaceti, which is situated over the skull, the content of which is largely constituted of waxes. The physiological function of this organ, however, has not yet been clarified. No other animals are known to possess spermaceti or any organ similar to it, except that the bottle-nosed whale has a small organ which is probably homologous to the spermaceti. As for the presence of large quantities of wax, similar instance is not known in any other animal than the two species named. Even in other whales, usual glycerides constitute the major part of the fatty substances together with a small amount of sterols and other unsaponified matters, as it is in the case in other animals. Ishikawa suggests this may be related to the diving ability.

Diving bradycardia has not been observed in the porpoises and probably does not take place in the greater whales. Perhaps one of the explanations as to why bradycardia is not necessary in the whale is the retia mirabilia. The retia mirabilia are the most remarkable anatomical features in whales. These vascular networks have been noticed by many anatomists and have caused much speculation.

The thoracic rete is the vast and long-extended mass of networks of the vascular capillaries, located along the vertebral column from the 1st cervical to the 6th dorsal vertebra. These networks moreover, pass between the transverse processes into the neural canal where they are in connection with the intraspinal retia. The basicranial rete lies at the base of the skull.

The rete is the dense mass of networks of vascular capillaries which are in open communication everywhere with certain arteries and veins, embedded in its capillary system. This capillary system of the rete is supplied with blood by its own arteries from the main arterial system and drained through its own veins into the main venous system. The rete does not impede the blood flow on the course of main blood vessels, but intervenes between the main arteries and veins. In this respect, it gives an impression of the arterio-venous shunt, but it is not merely the constrictor mechanism. The rete is as a whole, embedded in a large quantity of fat and enveloped in stout connective tissues. Thus, it has no relation with any surrounding organs or tissues, and therefore it appears to be an independent organ.

The retia mirabilia or structures similar to these, are found in all mammals which are capable of diving and of staying submerged for long periods, that is, in seals, porpoises, dolphins, and whales. Animals in the order Sirenia, which do not have the habit of remaining submerged so long, do not possess these vascular networks.

Ommanney is of the opinion that these vascular networks are most likely to be concerned in some way with gaseous exchange. He said,

In this connection, the situation of the networks near the respiratory center and on the course of main blood vessels and also around the brain and nerve chord is extremely suggestive. It has already been mentioned

that the masses of the rete are abundantly charged with fat. Oxygen is very soluble in fats. It may be imagined that some chemical mechanism exists for a more speedy transfer of oxygen from the blood to the fatty masses of the retia, which may thus act as an oxygen storage mechanism. The retia may in fact be capable of forming a sort of accessory lung. Since the vascular networks are under the control of the somatic nervous system, they may possibly be engorged with blood at will from the posterior thoracic artery, and this blood may perhaps be discharged at will again into the posterior thoracic vein. (Ishikawa, 1961).

The avoidance of caissons disease in the diving animals can be explained by the fact that a diving animal does not carry enough air for a serious supersaturation in a single dive, and the chance of supersaturation from repeated dives is lessened by restricted circulation during the dives, in some, followed by profuse circulation and hyperventilation in the recovery.

An interesting line of adaption in some the diving animals has taken place as a result of their infrequent breathing. In manatees, porpoises, and whales, the rate may be from one to three times a minute, or even less during periods between sounding. This infrequent breathing has resulted in utilization of a very large part of the total lung volume for tidal air, especially in cetaceans. Tidal air is that amount of air usually taken during a normal inspiration. The bottle-nose porpoise, Tursiops, for instance, uses some 80% to 90% of the total lung volume for normal tidal air and hence can increase ventilation only by increasing the frequency of breathing. Indeed, in so doing it tends to lose some efficiency through slightly shallower inspirations. The oblique position of the diaphragm and the soft thorax brings about a dorsiventral compression of the lungs and makes possible the extremely small amount of residual air after a normal expiration. This, in fact, is what makes possible a complete lung

collapse in deep diving. The very complete air renewal facilitates high utilization of the alveolar oxygen, amounting to some 8 to 10 per cent in whales with a corresponding 6 to 8 per cent carbon dioxide in the exhaled air, i.e., figures just about the double of those in man. Seals are intermediate in this respect.

It is natural to assume that the pulmonary system of the seal or whale collapses in a sequence determined by the stiffness of the various parts, or in such a way that the alveoli are the first to collapse, emptying their air into the tracheae and bronchi which ultimately flatten, delivering their air into the bony passages within the skull. If such a collapse were to be resisted, for instance, by a stiff chest wall or bronchi, blood and edema would gorge these air spaces. Ultimately the chest would fracture and cave in. It is obvious therefore that, as observed, the deep-diving animals must have provisions for full collapse of the lungs, and this will of course slow down the invasion rate of nitrogen because of elimination or reduction of the alveolar surface. It so happens that seals usually expire when they dive, and alveolar collapse takes place at a depth of some 30 to 40 meters. Collapse in whales, which usually dive on inspiration, will occur at 100 to 200 meters. Below these depths the nitrogen invasion would be very slow (Scholander, 1964).

CHAPTER IV

DIVING ADAPTATIONS SHOWN BY MAN

Man also shows some of the adaptations to diving. Northern Australian pearl divers show bradycardia. The diver develops bradycardia within 20 to 30 seconds after submersion whether quiet or actively swimming. During the dive the arterial blood pressure is normal or even elevated. However, the diastolic pressure drop is slowed down apparently by constriction of peripheral blood vessels. Little or no lactic acid is found in the blood during the dive, but there is an acute rise in the blood level concentration during the recovery period. Humans show one unique characteristic so far not found in other animals. Pathological arrhythmias or irregularities of the heart beat are common after only one half of a minute of submergence (Scholander, 1963).

Cardiac arrhythmias occurred with 45 of 64 periods of apnea in 16 subjects and were more frequent during actual dives than during breath holding. These arrhythmias, with the exception of atrial, nodal and ventricular premature contractions, were inhibitory in type and included sinus bradycardia and arrhythmia, sinus arrest followed by either nodal escape or ventricular escape, Auricular-Ventricular block, Auricular-Ventricular nodal rhythm, and idioventricular rhythm. Prompt return to normal sinus rhythm was the rule with the first breath after surfacing. Sinus tachycardia, sinus arrhythmia, and atrial,

nodal, or ventricular premature constrictions were seen during recovery (Olsen, 1962).

Bradycardia has been observed in humans of all ages regardless of the depth. However, it does not appear in compression chambers. It was more apparent in cooler water than in warm water (Craig, 1963).

Elsner at Scripps Institute has been able to demonstrate ischemia or lack of blood flow in the muscles of the extremities by having a volunteer submerge his face in a basin of water. As soon as the subject immerses his face his heart beat slows down. There is virtually a stop in the blood flow into the calf. As soon as the subject lifts his face out of the water and breathes the arterioles open again and the blood flows. If the subject is told to hold his breath without submerging his face, all the effects are less pronounced. Bradycardia is also shown by babies during difficult deliveries when the delivery time is longer than normal (Scholander, 1963).

CHAPTER V

SUMMARY

It has been pointed out in this paper that diving vertebrates show some adaptations to the threat of asphyxia due to prolonged dives. The most universal adaptation is bradycardia or slowing down of the heart beat rate. This has been shown to occur in nearly all diving animals studied, and also in some non-diving animals. Diving snakes, alligators, seals, beaver, some turtles, and several others including man show this adaptation. Along with the bradycardia, vasoconstriction is also found. The muscles, kidneys, intestines, and other areas show the constriction. The heart and brain, which have very little tolerance for anoxia, during this time has normal or even increased blood flow.

A reduction of metabolic rate in the peripheral tissues is another adaptation found in the diving vertebrates. This is evident by the drop in body temperature in these natural divers. When vasoconstriction of the tissues occurs, the metabolic rate is jammed by the lack of blood. The results of the adaptations, here mentioned, is to reduce the diving animal to a heart-brain-lung preparation, or a "smaller animal". The effect is to provide the tissues that are not tolerant to asphyxia - heart and brain - with the most optimum environment possible under diving conditions.

Some diving animals show other adaptations. The freshwater

turtle survives prolonged diving due to anaerobic glycolysis plus an adaption in the ventricular septum that allows a shunting of the blood. The whale and porpoises show no bradycardia, but do have an "organ" called the retia mirabilia or similar structures. This structure gives the impression of being an arterio-venous shunt which assists in prolonging diving. The high wax content in whales may also serve to help as does the spermaceti in sperm whales and a similar organ in the bottle-nosed whale. The bellows function in the diving animals is another adaptation that allows for deep diving without crushing the chest and warding off caissons disease.

These are all adaptations that help the diving vertebrates survive the threat of asphyxia due to prolonged diving.

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