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RESTRAINED AND UNRESTRAINED DIVING IN SEALS

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INTRODUCTION

In order to investigate the nature of the diving reflex or diving response in seals and to test hypotheses concerning the functions of various anatomical adaptations alleged to be associated with deep or prolonged diving it is necessary to dive seals under experimental conditions. Until recently information has been obtained largely from seals restrained in several ways and forcibly submerged at sea, in tanks (Fig. 31) and in pressure chambers. During such forced dives investigators have monitored heart rate, cardiac output, blood flow in large vessels, temperature changes and urine production, among other responses (Harrison et al., 1968; Ridgway, 1972).

Scholander (1940) first investigated forced diving in young *Halichoerus* and *Cystophora*, and since his experiments, the diving response has been followed in *Zalophus*, *Callorhinus*, *Phoca* and *Mirounga*. The results of these investigations were reviewed by Harrison and Kooyman (1968) who made a number of generalizations about the characteristics of diving bradycardia. Even though observations were scanty at that time, it seemed clear that diving bradycardia was less marked in unrestrained seals than in those restrained during forced dives. In most of these unrestrained experiments the seal was in a harness with trailing ECG leads (Harrison and Tomlinson, 1960).

Observations on restrained seals dived experimentally (see Harrison and Kooyman, 1968, p. 224) allow the conclusion that bradycardia is a component of a diving response which includes decreased cardiac output, peripheral arterial vasoconstriction and maintenance of blood pressure. Bradycardia develops rapidly in small phocids but less rapidly in larger forms (when drugged) such as *Mirounga*. It is more profound and its onset more abrupt in adults than in pups and yearlings. Bradycardia is also most marked when seals are dived restrained in pressure tanks. In young *Phoca* a steady increase in heart rate from the slowest rate has been noted towards the end of 20 min restrained dives,

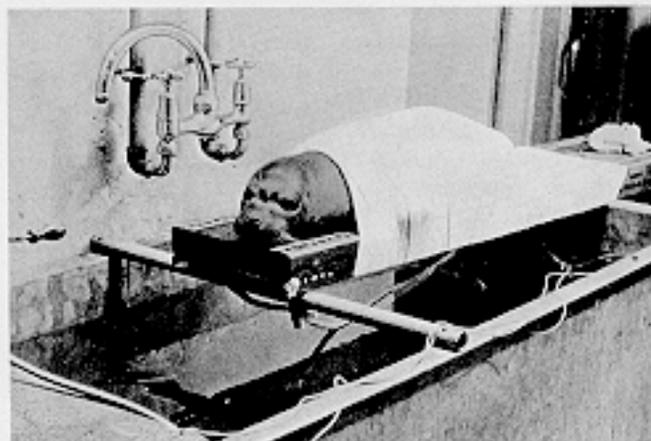


Figure 31. Young common seal (*Phoca vitulina*) secured to a board for shallow restrained dives (see Harrison and Tomlinson, 1960).

but in *Mirounga* the heart rate was slowest at the end of a 40 min dive. In otariids such as *Callorhinus* that dive for relatively short periods, bradycardia may not develop for up to $\frac{1}{2}$ min. This could indicate an optional aspect to the diving response, as though the animal could choose when to initiate it. Vagotomy abolishes bradycardia, and section of the right phrenic nerve supplying the caval sphincter delays the onset of bradycardia and inhibits a profound slowing of heart rate. In seals restrained out of water, short periods of bradycardia or cardiac arrhythmia can occur during respiration, on forced apnea, and as a result of many stimuli that cause a seal to hold its breath.

MATERIALS AND METHODS

Radiotelemetry devices have been implanted in the hypodermis of the back and neck of 12-18 month old grey seals (*Halichoerus grypus*) provided by Jon Gunnarsson of the Aquarium Hafnarfjordur, Iceland in order to follow heart rate changes in unrestrained seals trained to dive on command.

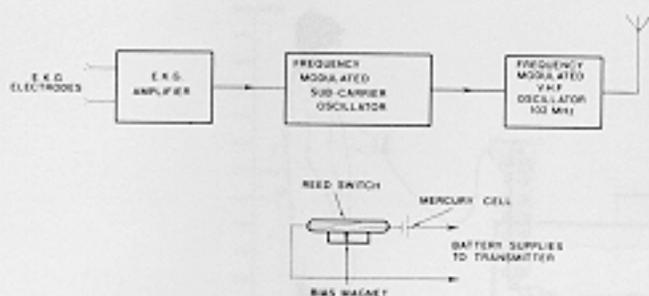


Figure 32. Plan of transmitter components as constructed by Mr P. L. Joyce, Physiological Laboratory, Cambridge University.

The transmitter comprised three stages (Fig. 32). A high input impedance pre-amplifier fed a pulsed frequency modulated sub-carrier oscillator, which in turn drove the frequency modulated transmitter stage. A carrier frequency of about 102 MHz was used allowing the signal to be received by a domestic FM receiver. The frequency modulated sub-carrier pulses from the receiver were converted to a standard width and integrated by a low-pass active filter to obtain the original input signal (Fryer and Deboo, 1964). The package had electrodes extending through the hypodermis across the thorax. The ECG could be broadcast continuously over a period of several months: an incorporated magnetic switch (Fig. 32) turned the transmitter on and off.

McGinnis (1968) suggested various sites in organs, such as the alimentary tract and the uterus, for the placement of EKG electrodes and the transmitter. A disadvantage of the stomach as a site is that presence of fluid can cause shorting between electrodes and loss of signal. We suspect that signals from the uterus would be too weak for our purposes. The most satisfactory site for placement of our transmitters has been at the base of the neck just cranial to the level of the anterior edges of the scapulae, although we have had good results over periods of up to two months with transmitters placed on the back and in the axilla. The danger is of stress on the repaired incision due to the seal's activity especially when climbing in and out of its pool. Activity may also put stress on the parts of the transmitter and cause leakage at weak points. Our present transmitters are packaged in a Teflon tube that has been etched and sealed with Araldite after the electronic components have been embedded in beeswax. The whole package is then ensheathed in silicone rubber (Fig. 33). Other methods to withstand mechanical stress and intrusion of body fluids are being investigated with the assistance of P. L. Joyce of the Physiology Laboratory, University of Cambridge.

Implantation of the transmitters made it possible to carry out prolonged experiments on EKG characteristics and changes in cardiac rhythm in relation to

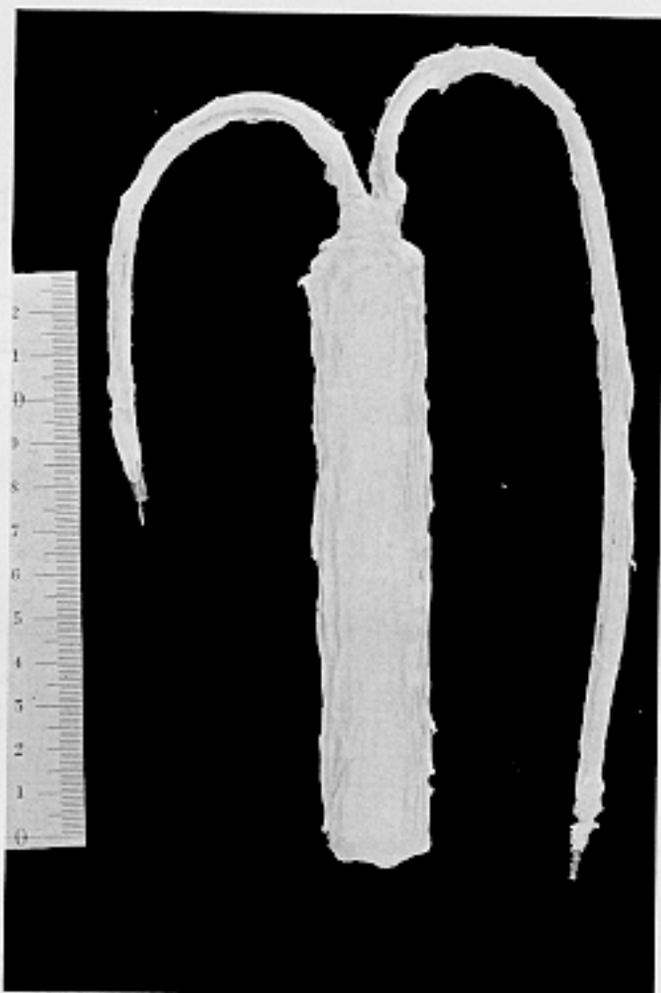


Figure 33. Photograph of EKG transmitter ready for implantation: scale in centimetres.

respiratory rhythm on land, during sleep, swimming and resting with head above water, and during diving in unrestrained seals, and to compare them with findings in restrained seals. Similar dives were carried out with seals containing transmitters but with the animals forcibly submerged in a cage lowered into a tank.

The seals were trained to submerge on command signalled by an underwater light (Fig. 34). When the light was turned off and a whistle sounded as a bridging stimulus, a fish was delivered by an underwater feeder. Thus the seals could be instructed to make voluntary dives of up to 8 min and recordings were made before, during and after the dives.

RESULTS AND DISCUSSION

The respiratory rate out of water was 2–12 per min. The heart rate was 120–150 beats per min but fell to

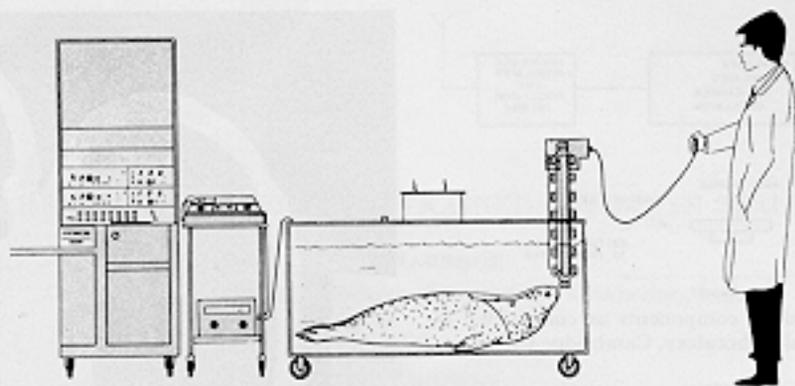


Figure 34. Diagram of experimental set-up for trained dives in a glass observation tank.

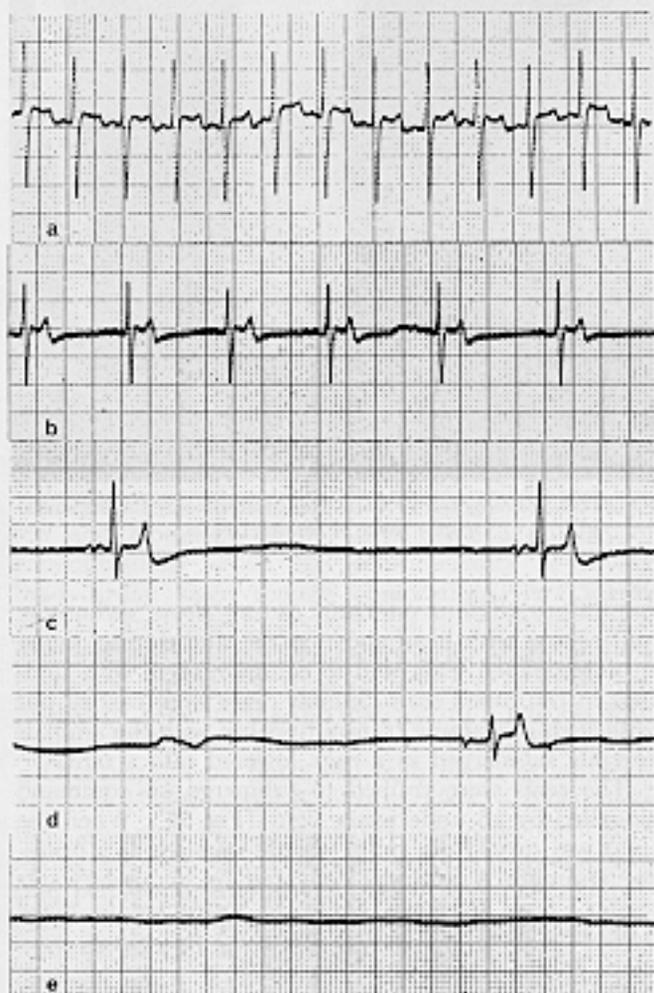


Figure 35. Extracts of EKG transmissions: (a) seal breathing (rate 150–180 b.p.m.), (b) seal out of water between breaths (rate 40–70 b.p.m.), (c) trained dive (rate 30–40 b.p.m.), (d) forced dive (rate 20–30 b.p.m.) and (e) forced dive when on occasion no beats occur for up to 8 secs.

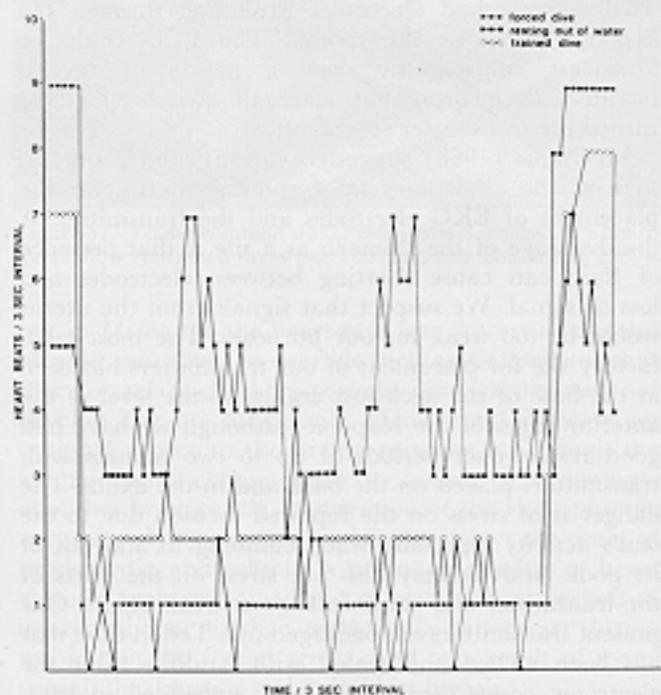


Figure 36. This graph shows the number of heart beats per 3 sec. interval under three different conditions. The upper line represents a seal resting out of water. The seal breathes one to three times, then holds its breath for 20–60 secs then breathes again. There is a reduction in heart rate to about 60 b.p.m. when the seal is not breathing. The next line represents a trained dive during which the heart rate immediately falls to 20–40 b.p.m. and remains at that level with occasional fluctuations to 60 b.p.m. The forced dive (lower line) is similar except that the average heart rate is slower.

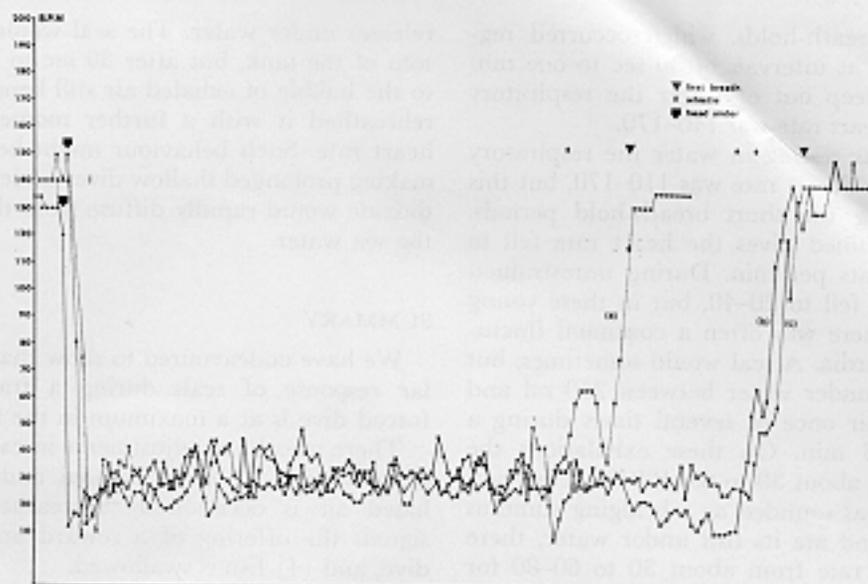


Figure 37. Three separate trained dives by a grey seal (a = 2 min 45 secs.; b = 3 min 3 secs.; c = 4 min 18 secs.). The EKG records were analyzed by measuring the interval between each QRS complex. Each point represents the delay between individual beats expressed in heart-rate per minute. Thus the horizontal axis represents the total number of beats during each of three dives and is not linear with time. Fluctuations in heart rate occur around a mean of about 30 per minute. When the end of the dive is signalled by a whistle the heart rate increases as the seal eats its fish reward, but starts to slow again as the animal surfaces, then shoots up immediately as the first breath is taken.

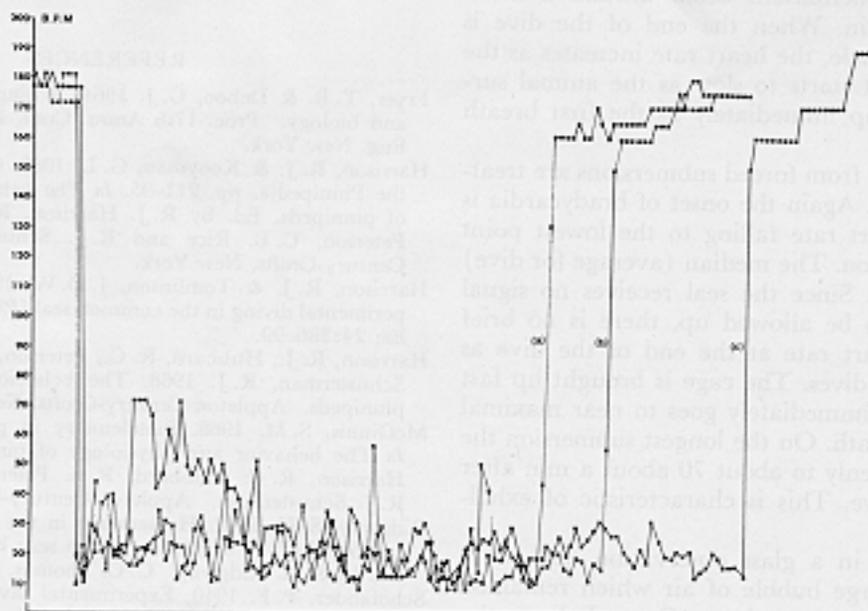


Figure 38. Forced dives by a grey seal (a = 6; b = 7; and c = 8 minutes). The EKG records were analyzed by measuring the interval between each QRS complex. Each point represents the delay between individual beats expressed in heart-rate per minute. Thus the horizontal axis represents the total number of beats during dives of 6, 7 and 8 minutes and is not linear with time. There were more beats in the 8 minute dive because the seal exhaled during the dive and the heart rate increased, giving the submersion a greater proportional number of beats than the 6 and 7 minute dives.

40-70 during the breath-holds, which occurred regularly for 30-50 sec at intervals of 30 sec to one min (Fig. 35). When asleep out of water the respiratory rate was 8-15 and heart rate was 140-170.

When the seal was resting in water the respiratory rate was 3-5 and the heart rate was 110-170, but this fell to 33-48 during the short breath-hold periods. During forced restrained dives the heart rate fell to as low as 10-40 beats per min. During unrestrained dives the heart rate fell to 20-40, but in these young trained grey seals there was often a continual fluctuation in the bradycardia. A seal would sometimes, but not always, exhale under water between 250 ml and about one litre of air once or several times during a trained dive of 2-8 min. On these exhalations the heart rate rose from about 30 to 65-100 for a few sec. When the whistle was sounded as a bridging stimulus and the seal took and ate its fish under water, there was a rise in heart rate from about 30 to 60-80 for a few sec. There followed a sharp fall in heart rate for a further few seconds while the seal returned to the surface, when heart rate immediately rose to 150-180 (Fig. 36).

In order to determine if there were any consistent trends or small changes in heart rate during a dive we analysed some of the records by measuring the interval between every QRS complex of the EKG. In Figure 37 three separate trained dives are compared. In every case the heart rate falls immediately to near its lowest point. Fluctuations occur around a mean of about 30 per min. When the end of the dive is signalled by the whistle, the heart rate increases as the seal eats its fish but starts to slow as the animal surfaces, then shoots up immediately as the first breath is taken.

In Figure 38 data from forced submersions are treated in the same way. Again the onset of bradycardia is immediate, the heart rate falling to the lowest point during the submersion. The median (average for dive) heart rate is lower. Since the seal receives no signal when it is going to be allowed up, there is no brief rise and fall in heart rate at the end of the dive as seen in the trained dives. The cage is brought up fast and the heart rate immediately goes to near maximal rate on the first breath. On the longest submersion the rate increased suddenly to about 70 about a min after the start of the dive. This is characteristic of exhalation under water.

Seals submerged in a glass observation tank were seen to exhale a large bubble of air which remained beneath the surface glass sheet. On exhaling, the heart rate rose momentarily as during other breath

releases under water. The seal would dive to the bottom of the tank, but after 30 sec to 1 min it returned to the bubble of exhaled air still beneath the glass and rebreathed it with a further momentary increase of heart rate. Such behaviour might be of value to seals making prolonged shallow dives under ice, since carbon dioxide would rapidly diffuse from the air bubble into the sea water.

SUMMARY

We have endeavoured to show that the cardiovascular response of seals during a trained dive and a forced dive is at a maximum in the forced dive.

There are also readjustments in cardiac rhythm that occur when (1) air is exhaled under water, (2) exhaled air is occasionally rebreathed, (3) a whistle signals the offering of a reward and the end of the dive, and (4) fish is swallowed.

It is essential that we understand the normal diving responses of the unrestrained seal before we can understand the anatomical specializations that are purported to be involved in diving, such as the caval sphincter and the extradural veins. Prolonged observations of trained seals resting in or out of water, asleep, and diving at will suggest that there is a facultative element in the response, and that a seal may well be capable of adjusting the response to different types of dives.

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