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The effects of breathing different levels of O_2 and CO_2 on the diving responses of ducks (*Anas platyrhynchos*) and cormorants (*Phalacrocorax auritus*)

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Summary. The effects of breathing different levels of O_2 and CO_2 before forced dives were investigated in 5 dabbling ducks (White Pekin) and 5 deep divers (Double Crested Cormorants). Breathing and heart rates, blood gases, and blood pH, were monitored. After breathing air before diving, ducks exhibited a slow decrease in heart rate that reached a minimum of 20 beats·min^{-1} after 50 s submergence. The development of bradycardia was retarded if the duck breathed a hyperoxic gas mixture before diving and was accelerated if the gas mixture was hypoxic and hypercapnic. The cormorants' diving heart rate decreased to a minimum of about 60 beats·min^{-1} in less than 20 s and development of bradycardia was unaffected by different levels of O_2 and CO_2 breathed before diving. Consequently, bradycardia in forced dived cormorants was unrelated to changes in blood gases in the dives which suggests that intravascular chemoreceptors are unimportant in initiating diving bradycardia in cormorants.

Introduction

Since 1870, when Paul Bert described the apnea and the profound bradycardia which occurs in the forcibly submerged duck, this animal has been a favorite in the study of the diving reflex. The domestic duck does not dive, however; it submerges only its head and neck, the body remaining at one atmosphere pressure and the P_{O_2} and P_{CO_2} in the lungs and blood accurately indicating the actual O_2 used and CO_2 produced. This allows input from intravascular chemoreceptors to be the major control of heart rate in these birds (Jones and Purves 1970; Lillo and Jones 1982) and diving bradycardia develops slowly along with the decline in blood O_2 tension.

In a deep diver like the cormorant, the partial pressure of a gas in the lungs, and blood, will rise in proportion to the total pressure (Dalton's Law). This has been shown to occur in penguins during simulated deep dives by Kooyman et al. (1973). The gas tensions (but obviously not content) in the lungs would increase by one atmosphere with every 10 m of depth and thus intravascular chemoreceptors, which react to gas tensions, would respond inappropriately, especially at the beginning of a dive when the Pa_{O_2} is very high and Pa_{CO_2} is relatively low. Additionally, it would make little sense for a deep diver to wait for Pa_{O_2} to decrease before initiating O_2-conserving reflexes. If the cormorant does not rely on chemoreceptor input to control heart rate during a dive, then the P_{O_2} or P_{CO_2} of the blood should have no effect on the development of diving bradycardia.

To test the hypothesis that the cormorant's chemoreceptors have reduced importance in determining diving heart rate, both ducks and cormorants were allowed to breathe various mixtures of O_2 and CO_2 before a dive. The ducks provide chemoreceptor-mediated cardiovascular responses to submergence to which the cormorants' responses can be compared.

Materials and methods

Five Pekin ducks (*Anas platyrhynchos*) and five Double Crested cormorants (*Phalacrocorax auritus*) of both sexes (average weights 2.95+0.06 kg and 2.00±0.09 kg, respectively) were used. Both species were kept in outdoor pens; no attempt was made to acclimate the birds to the experimental temperature which was about 5 °C above the outdoor temperature at the time.

The birds were restrained prone, by taping them loosely to a metal frame. Heart rate was measured from the ECG, breathing rate by an electronic thermometer with a remote thermistor probe. The probe was placed over the nares in the duck; in the cormorant, which lacks external nares, the probe

was taped to the lower bill and extended down the gullet until the tip was about 0.5 cm above the glottis. Because the probe was taped securely to the bill, it did not touch the glottis and the breathing rate was unaffected.

The gases administered to the birds were 50% oxygen (D1, C1), air (D2, C2) and a hypoxic, hypercapnic mixture (D3 11.9% O_2, 4% CO_2; C3 12.8% O_2, 3% CO_2) and were delivered to the birds at a rate of 1.6 ± 0.2 l·min^{-1} via a plastic bag fastened around the diving apparatus and neck of the bird. To determine what the bird was actually breathing before a dive, samples of gas were taken periodically from the bag and analyzed.

Before a set of dives, the bird's head was immobilized in a brace and lowered into an opaque funnel for at least 5 min before the dive started. A control dive was done first, after a period in which the bird had breathed air freely. The other gases were given, and associated dives performed, in random order. The test gas mixture was administered for at least 5 min before the dive, which was initiated by filling the funnel. The dives lasted about 120 s for both species, being terminated by draining the funnel. During recovery, the bird's head was not raised and it continued to breathe the same gas as it had predive. One trial was conducted on each bird at each gas mixture.

Three 0.75 ml blood samples were taken from a brachial artery to test blood gas tensions and pH, one at 30 s before the dive, one each bracketing 30 and 120 s into the dive. Sampling time was less than 10 s per sample. The samples were heparinized, capped, and placed on ice for no longer than 7 min before they were analyzed. Blood samples were analyzed at 41 °C with an IL Micro 13 Blood Gas Analyzer, recalibrated before every sample.

The cardiac rates were averaged over 4 s intervals, the breathing rates, over 10 s. The UBC ANOVAR program was used to generate the Anova tables for cardiac data, and perform multiple range tests to determine homogenous groups of heart rates across treatments. Student's *t*-test was used to compare paired data between species. Significance was set at the 95% confidence level ($P<0.05$). A value associated with a mean indicates the standard error of the mean. There were no significant differences between the dives in which air was breathed freely (control dives mentioned above) and those in which air was administered. Therefore, in all comparisons among dives, values (D2, C2) are those obtained from dives after air administration. The designation of the gas breathed before the dive is used in referring to the diving trials.

Results

Changes in heart rate

Both species' resting heart rates were unaffected by different levels of O_2 and CO_2 in the gas breathed before the dive. The ducks' resting rates ranged from 184 to 216 (average 202) beats·min^{-1} (Fig. 1a), the cormorants', from 152 to 188 (average 168) beats·min^{-1} (Fig. 1b).

The effect of the different gases on the resting breathing rates in both species was slight. In both ducks and cormorants, the resting rate was elevated by about 3–4 breaths·min^{-1} when the birds were breathing hypoxic-hypercapnic gas mixtures. When breathing comparable gases, the breathing rate in ducks (10.7 ± 1.1 breaths·min^{-1}, breathing

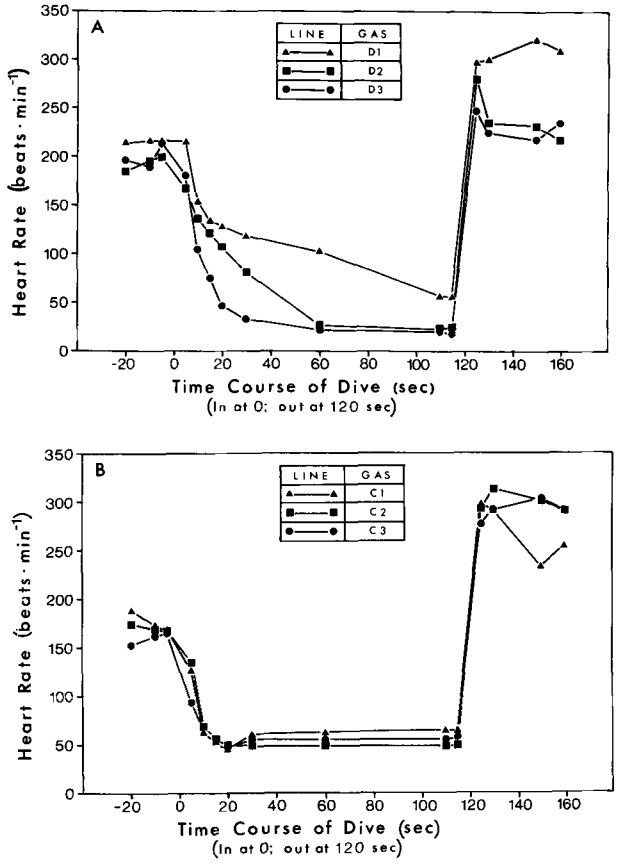

Fig. 1 A, B. Changes in heart rate in the duck (**A**) and cormorant (**B**). The composition of the gas breathed before diving was 50% O_2 in D1, C1; air in D2, C2; 11.9% O_2 and 4% CO_2 in D3 and 12.8% O_2 and 3% CO_2 in C3

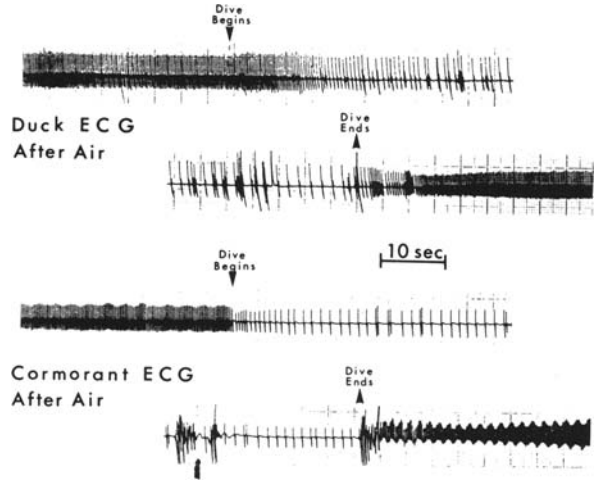

Fig. 2. Duck and cormorant ECGs taken after the birds had breathed air (gases D2 and C2), showing the difference in the initiation of bradycardia. The dives are approximately 60 s long, which was half the length used in the present experiments. The cormorant record is continuous; 4 s in the middle of the duck record has been omitted in aligning the dives

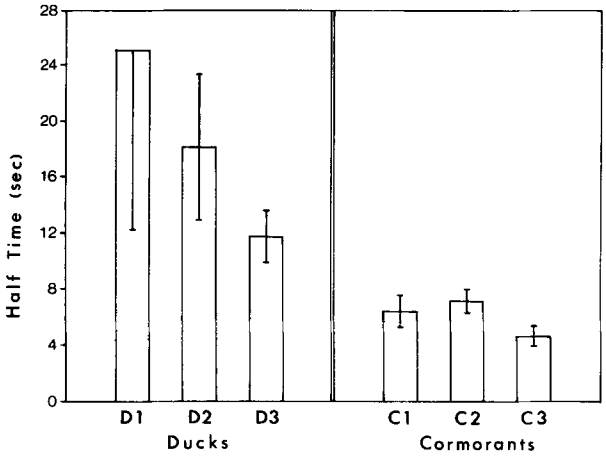

Fig. 3. Heart rate half times for ducks and cormorants. The half time is the time, from submersion, for the heart rate to fall to one half the difference between resting and the minimum heart rate. Gas compositions breathed before diving are given in the legend to Fig. 1

air) was about half that in cormorants (22.5 ± 3.2 breaths·min^{-1}, breathing air). This difference was significant for all trials.

The onset of bradycardia was significantly faster in cormorants. Over the first 10 s, heart rate in the cormorants decreased an average 99.3 beats·min^{-1}; heart rate in the ducks decreased by an average 76.0 beats·min^{-1} (Fig. 2). This difference is reflected in the half times, which is the time from submersion, for the heart rate to drop to one half the difference between resting and minimum diving heart rate (Fig. 3). The average half times for the ducks increased as the O_2 concentration of the gas breathed pre-dive increased, but the average half time for dive D1 (25.1 ± 13.0 s) was not significantly greater than those of the other dives (18.1 ± 5.2 s (D2), 11.8 ± 1.9 s (D3)). (In a previous study, with a larger sample size (Mangalam 1980), the half time for dive D1 was significantly greater than the others.) The cormorant half times were not significantly different from each other, but they were significantly faster than those of the ducks. For the cormorant dives C1, C2, and C3, the half times were 6.4 ± 1.1, 7.2 ± 0.8, and 4.7 ± 0.7 s, respectively.

The minimum diving heart rates (the lowest heart rate averaged over 20 s) for the cormorants ranged from 64.8 ± 8.4 (C1) to 56.7 ± 5.2 (C2) beats·min^{-1}. Although these were not significantly different from each other, the average diving heart rate, after breathing O_2 pre-dive, was consistently higher than the diving heart rates following the other two gases. The minimum diving heart rates in the ducks were 54.0 ± 9.1 (D1), 20.5 ± 2.8 (D2), and 18.6 ± 2.4 (D3) beats·min^{-1}. The minimum diving heart rate in trial D1 (50% O_2) was significantly higher than those in the other duck dives.

The post-dive increase in heart rate in any trial was not significantly different between ducks (22.9–25.5 beats·min^{-1}·s^{-1}) and cormorants (21.9–24.4 beats·min^{-1}·s^{-1}). In both species, the recovery tachycardia was dependent on the resumption of breathing. Both species re-established the pre-dive resting heart rate within 7 min; one species did not recover significantly faster than the other.

Pa_{O_2}, Pa_{CO_2}, and pH changes

The Pa_{O_2} in both species decreased more rapidly in the first 30 s of submersion than in the last 90 s in all dives (Fig. 4A, B). Breathing the hyperoxic gas (D1, C1) before the dive dramatically increased the pre-dive Pa_{O_2} by an average 142 mm Hg in the cormorants, by 152 mm Hg in the ducks. Pa_{O_2} remained significantly above normal (D2, C2) levels throughout the dive in both species. The cormorants' Pa_{O_2} remained significantly higher in dive C2 than in dive C3 but there was no such difference in corresponding duck trials.

The Pa_{O_2} in the first 30 s of the dive, after breathing 50% oxygen, fell by an average of 67 mm Hg in the duck, by 12 mm Hg in the cormorant. The average falls in Pa_{O_2} after a 2 min dive were less variable in the cormorants than in the ducks. Overall, the cormorants' Pa_{O_2} fell by an average of 42 mm Hg in dive C1, 36 mm Hg in C2, and 38 mm Hg in C3. The ducks' Pa_{O_2} fell an average of 92 mm Hg in dive D1, 37 mm Hg in D2, and 29 mm Hg in D3.

Pa_{CO_2} increased almost linearly through the course of the dive in both species (Fig. 4A, B). Pa_{CO_2} in diving cormorants was consistently lower after breathing air pre-dive, both at 30 s and 120 s, than after breathing the other two gases pre-dive. Pa_{CO_2} in both species was highest at the 120 s point after breathing 50% O_2 pre-dive (D1, C1). In the cormorants, the Pa_{CO_2} rose an average of 42 mm Hg in trial C1, 32 mm Hg in C2, and 31 mm Hg in C3. In the ducks, Pa_{CO_2} rose an average of 39 mm Hg in trial D1, 31 mm Hg in D2, and 20 mm Hg in D3.

Blood pH decreased through the dive (Fig. 4A, B), more quickly in the first 30 s than in the last 90 s in all of the dives except one; in dive C1, pH fell more rapidly in the later period (Fig. 4A, b and B, b). In ducks, pH fell an average of 0.19 pH units in dive D1, 0.17 pH units in D2, and 0.16 units in D3. In the cormorants, pH fell

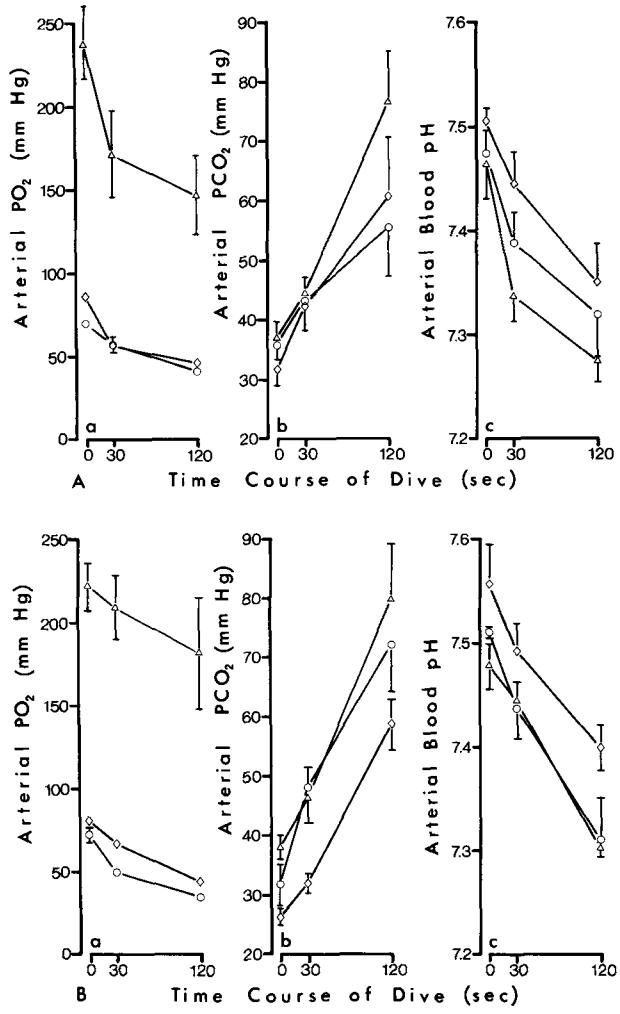

Fig. 4A, B. Arterial blood gas and pH changes in the duck (**A**) and the cormorant (**B**) during diving. Symbols without error bars are larger than the associated error. Key: Triangles (△) – dives D1, C1; Diamonds (◇) – dives D2, C2; Circles (○) – dives D3, C3. The gas compositions breathed before diving are given in the legend of Fig. 1

an average of 0.18 pH units in dive C1, 0.16 pH units in C2, and 0.20 pH units in C3. In both species, breathing air before the dive resulted in the most basic blood, breathing 50% O_2 in the most acidic blood, both pre-dive and during submergence.

Discussion

This study has shown that the development of diving bradycardia in the duck is considerably delayed by increasing the concentration of O_2 in the gas that is breathed pre-dive. Bradycardia developed more slowly after breathing 50% O_2 than after breathing air or hypoxic and hypercapnic gas before diving. In contrast, in cormorants, maximum bradycardia was reached at similar times in all trials. In ducks, it is known that the major part of bradycardia is due to input from peripheral chemoreceptors (Jones and Purves 1970; Jones et al. 1982; Lillo and Jones 1982), however, the cormorants' responses suggest that chemoreceptors are unimportant in initiating their diving bradycardia.

In ducks, heart rate fell below 100 beats·min^{-1} after 20–30 s submergence, even after breathing 100% O_2 before the dive. This does not necessarily argue against the predominant role of chemoreceptors because Pa_{CO_2} rose to such spectacular levels in these dives. High Pa_{CO_2} stimulates both central and peripheral chemoreceptors to initiate the O_2 conserving cardiovascular responses in ducks (Jones et al. 1982). Obviously, in cormorants, bradycardia is initiated and probably maintained by other mechanisms which may involve receptors in the beak, or both central and peripheral respiratory related nervous activities. Certainly, these mechanisms can predominate in mammals (Dykes 1974a, b; Drummond and Jones 1979) and have been claimed to have some effect on the development of bradycardia in ducks (Andersen 1963; Jones and Butler 1982).

From the Pa_{O_2} and Pa_{CO_2} changes observed during diving, it might be concluded that ducks and cormorants do not differ significantly in their ability to conserve O_2 when diving after breathing air, which is unexpected because of the cormorants' more rapid development of bradycardia and potentially more rapid deployment of the oxygen conserving response. Although differences in volume of the respiratory system could be important, the actual blood oxygen content at a given dive Pa_{O_2} depends on a number of factors, including the P_{50} and Bohr shift, which are unlikely to be the same in cormorants and ducks. However, after breathing pure oxygen, Pa_{O_2} is so high both before and during dives that all oxygen will be used from physical solution in the blood and changes in Pa_{O_2} will provide a better indication of oxygen utilization. Since cormorants exhibit full bradycardia, compared with the much reduced bradycardia in ducks, the role of the diving reflex in oxygen conservation should be amplified. Consequently, if non-blood oxygen stores are similar in ducks and cormorants, it is no surprise that at the end of the post-oxygen dives (D1 and C1), Pa_{O_2} in the cormorants was much higher than in the ducks, indicating the efficacy of the oxygen conserving reflexes in forced diving. This is especially noticeable in the first 30 s of the dive (D1, C1), where the ducks' Pa_{O_2} falls precipitously compared to the cormorants' decline in Pa_{O_2} (Fig. 4).

Rapid onset of bradycardia is not a unique feature of cormorants for it is also shown in other diving birds submerging voluntarily. Unfortunately, the relationship between the forced and free diving response is not well documented although both Butler and Wakes (1979) and Kanwisher et al. (1981) have telemetered heart rates from freely diving cormorants and ducks. These studies show that the diving birds generally perform dives in a series, each dive being less than one minute long. Surface heart rates double between dives in the series and upon submergence, heart rate rapidly falls, but only to the resting level in both diving ducks and cormorants. Obviously, the potential for rapid falls in heart rate exists in diving birds, both in the field and laboratory (Catlett and Johnson 1974), but rapid onset of bradycardia is seldom seen in dabbling ducks forcibly submerged under laboratory conditions.

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