

GAS EXCHANGE AND ITS EFFECT
ON BLOOD GAS CONCENTRATIONS IN THE AMPHIBIAN,
XENOPUS LAEVIS

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INTRODUCTION

The overall regulation of gas transfer in an amphibian such as *Xenopus*, which has two sites for gas exchange and breathes only intermittently, must be complex. Such animals do not achieve the degree of homeostasis seen in mammals in which continuous breathing results in stable oxygen and carbon dioxide concentrations in the blood. There is a lack of agreement in the published values for oxygen exchange through skin and lungs (including buccal cavity), probably because of the different conditions under which they were determined (Jones, 1967; Hutchison, Whitford & Kohl, 1968). There is little doubt, however, that a considerable difference exists between values obtained when the animal is breathing air and when it is under water (Jones, 1967).

The amount of gas transferred through skin and lungs will be determined, amongst other things, by the extent to which these surfaces are ventilated by water or air and perfused by venous blood. Clearly lung ventilation must be intermittent since it is related to the diving-emergence sequence, and even at the surface the amphibian rarely ventilates its lungs in a continuously rhythmic fashion. Gas exchange through lung epithelium need not cease in the intervals between breaths if the lung is used as a store. Jones (1967) found that oxygen consumption in *Xenopus* was higher during the first 10 min of an enforced dive than it was during the rest of the dive or indeed during the time when the animal was at the surface. He suggested that the store of oxygen in the lungs was used during this period. The function of the lung as an oxygen store has not been firmly established. Even less is known about skin ventilation and the extent to which movements of the whole animal or its limbs are important in gas exchange at the skin.

Rather more information is available about perfusion of the gas exchangers. In recent studies on *Xenopus*, considerable fluctuation of pulmocutaneous blood flow was described which was related to the periods of lung ventilation. It was found that the vascular impedance of the pulmocutaneous periphery was very high between periods of lung ventilation but that it decreased sharply as soon as the animals breathed, leading to a fivefold to tenfold increase in pulmocutaneous blood flow (Shelton, 1970). Further investigations suggested that the variation of vascular impe-

dance was related both to the partial pressure of oxygen in the lungs and to the state of lung inflation (Emilio & Shelton, 1972). Though it was not possible to determine the skin blood flow independently from the pulmonary blood flow, it was assumed that the lung circulation rather than the skin circulation was affected as part of a general phenomenon of oxygen conservation. In fact Poczopko (1959) suggested that cutaneous vasodilation occurred during diving so that the decrease in pulmonary blood flow would be somewhat greater than the overall fall as recorded in the pulmocutaneous arch.

In order to quantify gas exchange at either of the two exchanging surfaces it is necessary to have some measure of oxygen and carbon dioxide contents of arterial and venous blood as well as determinations of blood flow rate. Very little work has been done to assess the normal values for gas contents or tensions in the blood of Amphibia. Most determinations have been made on terminal samples or in acute experiments on the selective distribution of blood to lung and body circuits (DeLong, 1962; Johansen, 1963; Johansen & Ditadi, 1966). Lenfant & Johansen (1967) measured the arterial oxygen and carbon dioxide tensions using chronically implanted catheters in three different species of Amphibia. They recorded a marked fall in arterial oxygen tensions when air-breathing forms were kept under water. Chronic experiments on *Amphiuma tridactylum* (Toews, Shelton & Randall, 1971) showed that substantial fluctuations of oxygen tension occurred in the blood from both systemic arch and pulmonary vein when the animal was free at all times to move to the water surface and breathe. Smaller changes were detected in blood from the pulmonary artery and inferior vena cava. However, the relationship between these fluctuations and total gas exchange was not examined.

The objective of the present work was to examine in more detail the role of the skin and lungs in transferring oxygen and carbon dioxide during breathing and diving periods. The effect of this transfer on blood oxygenation was also determined.

METHODS

The experiments were carried out, at room temperature (20 °C), on 47 healthy adult females of the species *Xenopus laevis*, weighing between 80 and 120 g. Twenty of the animals were used in direct measurements of gas exchange, made by putting an animal into an airtight perspex box containing known amounts of water and air. Small samples could be taken regularly for determination of the gas tensions in water and air using Radiometer oxygen (E 5046) and carbon dioxide (E 5037) electrodes in thermostatically controlled cells. An initial period of 20–40 min was allowed before starting the determinations so that the animals would be at rest, though they were not fully acclimated to the apparatus. The animals were kept for further experiments since they were not affected by the procedures described.

In five preliminary experiments a relatively large volume of air (200 ml) was included in the perspex box and the animal had free access to it for most of the time. The box was provided with an internal lid which could be lowered to the water level so that, for a short period in each experiment (20–40 min), the animal could not emerge to breathe. The area of the air–water interface was some 120 cm² when the animal had access to air, and this introduced error in determining the relationship

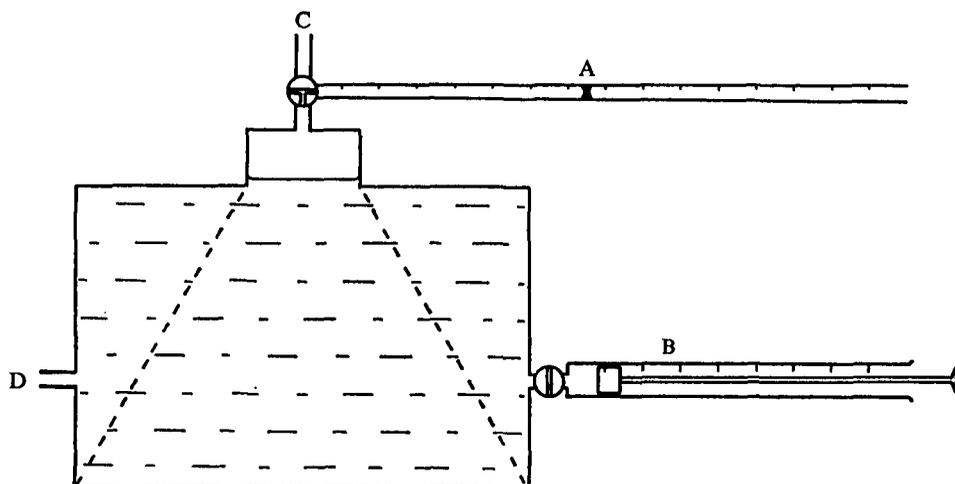


Fig. 1. Diagram of the apparatus used in determinations of oxygen consumption by the bubble technique. The meniscus in the pipette (A) was used to measure moment-to-moment changes of gas volume in the system. The water-filled cylinder (B) was used to renew the air in the bubble and to measure variations in lung volume at the end of each dive. The gas bubble could be analysed by means of oxygen and carbon dioxide electrodes (C). An oxygen electrode (D) was also used to monitor oxygen tension in the water. The broken line represents a wire mesh, used to guide the animal to the air bubble.

between oxygen consumption from air and water. In order to reduce movement of gas from one medium to the other through the interface, the apparatus was modified so that the box was full of water except for a bubble of known volume (10–15 ml) located in the middle of the lid (Fig. 1). The area of the air–water interface in this case was always less than 20 cm².

Initially it was assumed that the animal always dived with its lungs inflated to the same volume and that the amount of carbon dioxide given off from the lungs was negligible. The volume of oxygen in the bubble after each breathing period was determined by measuring its partial pressure, and the deficit was made good by introducing such volume of pure oxygen into the bubble as was necessary to restore the original partial pressure. The inaccuracies introduced by these assumptions were overcome by further modification of the apparatus as shown in Fig. 1, enabling the volume of the gas bubble to be measured before and after breathing periods. When the animal dived the bubble was expelled from the breathing chamber, through the oxygen and carbon dioxide electrodes, by depressing the piston in the water filled burette. The volume of gas in the bubble was measured by means of the graduations on this burette and the quantities of oxygen and carbon dioxide were calculated. A new air bubble of known size was then introduced into the chamber by withdrawing the piston, ready for the next emergence and breathing period. During the breathing period and early part of the dive the bubble was connected to the horizontally arranged, graduated, 1 ml pipette via the three-way tap. Any change in volume of the total system of bubble plus lung could be measured by means of a liquid meniscus in the pipette. Such changes would be produced when the volume of carbon dioxide given off to the gas phase was not equal to the oxygen taken up. In the diving animal any changes in lung volume would be communicated to the measuring system unless the animal

maintained a pressure difference across the lung and body wall. Variations in the final volume of the lungs towards the end of the diving period could be determined by reading the burette at the point where the bubble was completely expelled from the apparatus and comparing it with similar readings taken in earlier diving cycles.

Because the values for oxygen were somewhat different from previously published values (Jones, 1967; Hutchison *et al.* 1968) a manometric technique using two perspex chambers connected to a manometer (Jones, 1970) was employed to make determinations on a further ten animals. The gases in the air and water within the animal chambers were kept in equilibrium by means of a magnetically driven pump. This circulated water through fabric curtains suspended from the top of the tank and caused minimum disturbance to the water surface. Within this system, the oxygen gradient between air and water, produced by a respiring toad, was so small as to be not reliably measured by the electrode systems. Carbon dioxide was absorbed by soda lime and pressure differences between the animal chamber and thermobarometer of similar size were detected by a Sanborn 270 pressure transducer.

Water could be injected into the animal chamber from an automatic burette and the volume needed to minimize pressure differences between the two chambers was monitored as an experiment proceeded. The method resulted in progressive depletion of oxygen in the animal chamber but, as the level at the end of an experiment was about 90% of the initial value, this was not considered to be serious. The animals were free to move to and from the water surface and were acclimated to the box overnight. The apparatus was submerged in a water bath at 20 °C, and all necessary precautions for temperature and pressure equilibrium were taken.

The partial pressure of oxygen, and occasionally of carbon dioxide, in blood were determined in 17 animals. Branches of the cutaneous and of the femoral arteries were cannulated after anaesthesia by immersion in a tricaine solution (400 mg/l). Heparin (2 i.u. per 100 g body weight) was given to prevent blood clotting. The posterior end of the right lung was also cannulated in some cases. The surgical incisions were closed and the animal was allowed to recover from anaesthesia. It was then put into a small tank where it could swim freely, and the cannulae were connected to the thermostatically controlled chambers of two oxygen electrodes (Radiometer E 5046) or, in a few experiments, to one oxygen and one carbon dioxide electrode (Radiometer E 5037). Blood samples were taken at intervals, and returned to the circulation after readings of the partial pressures of the gases were recorded. A negligible amount of blood was lost in these conditions and each animal could be kept under observation for several days. The animals were sacrificed at the end of the experiments and in eight cases 3–4 ml of blood were withdrawn from the heart for determinations of oxygen and carbon dioxide contents. The blood oxygen dissociation curves were obtained by equilibrating small samples of blood with gas mixtures containing the required partial pressures of oxygen and carbon dioxide in a Radiometer BMS 2 thermostatically controlled microtonometer. The samples were analysed for O₂ and CO₂ contents in a Natelson microgasometer, using the standard procedures. A Radiometer Acid Base Analyser PHM 71 with oxygen and carbon dioxide modules was used for all the determinations of partial pressures of these gases.

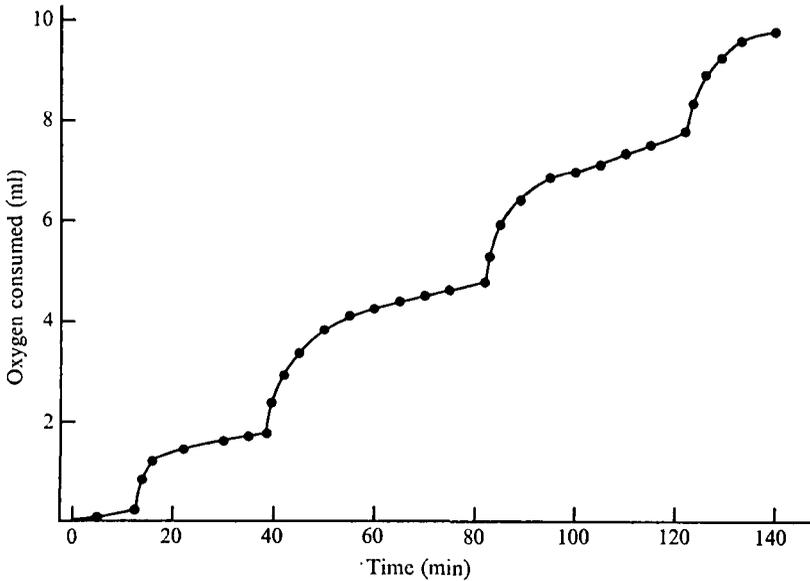


Fig. 2. Oxygen consumption of *Xenopus* (103 g) at 20 °C, as measured by the manometric technique. In the steeply rising sections of the plot, when the animal was breathing air at the surface, three times the number of points illustrated was obtained but these are omitted for clarity.

RESULTS

(i) Oxygen consumption from air and water

The breathing pattern of *Xenopus* observed under our experimental conditions was often irregular. Sometimes the animals would be immersed for periods up to 30–40 min or even more (Fig. 2), while on other occasions they emerged every few minutes and kept breathing for considerable periods of time. These extremes, or intermediate variations, could frequently be seen in the same animal as an experiment proceeded (Fig. 3).

The results for total oxygen consumption obtained in the three different types of determination do not differ from one another significantly. The figures obtained (Table 1) by summing the skin and lung values in the electrode experiments and from the overall slope of the curve of O_2 consumption in the manometric experiments lie between the values given by Hutchison *et al.* (1968) and Jones (1967). The skin and lung components in this total uptake show rather wider variation, almost certainly due to experimental method. In particular, significant differences exist between the value for skin oxygen uptake as measured by the manometric technique and those from the electrode experiments when the animal had access to the surface (Table 1, values 2–4 and 3–4). The former were determined from the slope of the oxygen consumption line when the animal was submerged (Fig. 2) and would be too high if oxygen was absorbed from the lung in the earlier stages of submergence. The latter would be too low because of diffusion of oxygen from air to water during the experiment. The value of $1.1 \text{ ml } O_2 \text{ h}^{-1} 100 \text{ g}^{-1}$ obtained when the *Xenopus* were submerged by a lid being lowered to water level is not affected by these deficiencies. Our attempts to see whether the rate of oxygen consumption from the water was increased when the toads were prevented from breathing air were not reliable because of these problems. The

Table 1. *Xenopus* oxygen consumption at 20 °C

	(ml O ₂ 100 g ⁻¹ h ⁻¹ ± s.d.)		
	Total O ₂	Skin O ₂	Lungs O ₂
Electrode experiments			
Large surface area (5 expts)			
(1) No access to air	—	1.1 ± 0.2	—
(2) Access to air	4.2 ± 1.0	0.6 ± 0.1	3.6 ± 1.4
Bubble technique (15 expts)			
(3) Access to air	4.8 ± 0.9	0.9 ± 0.3	3.9 ± 1.3
Manometric experiments (10 expts)			
(4) Access to air	4.5 ± 0.6	1.5 ± 0.4	3.0 ± 0.5
Probabilities of differences between means			
Values 1-3	—	< 0.7	—
Values 2-4	< 0.7	< 0.01	< 0.3
Values 3-4	< 0.7	< 0.01	< 0.1

difference between results obtained when the animals were allowed or denied access to air (Table 1, values 1 and 2) must be due largely to diffusion through the air-water interface. In fact, when the surface for diffusion was reduced in the bubble experiments there was no significant difference between the 'access' and 'no-access' figures (Table 1, values 1 and 3). The results suggest that there is no substantial increase in skin uptake when the animals are submerged.

The results for lung oxygen consumption (Table 1) do not differ significantly from one another, though it is likely that the value from the manometric experiments derived by subtracting skin values from the total figure is low for reasons already given. In the experiments in which the bubble technique was used, it was found that the volume, as measured by the burette during each bubble renewal when the animal was submerged, could vary by 1 or 2 ml. This indicates that the animals were diving at varying degrees of lung inflation. The fluctuation was rather irregular; for example, an animal could take in an excess of 2 or 3 ml of air in successive breathing periods and expel part or whole of the excess in a following breath. This is illustrated in Fig. 3, where the upper line represents the fluctuations of the total body volume of one animal as measured towards the end of 14 diving periods. These fluctuations are as large as the reported lung tidal volume of *Xenopus* of similar size (Hutchison *et al.* 1968). The measurement, by means of the pipette meniscus, of changes in volume of the gas phase during each breathing-diving sequence gave some information about the rate of transfer of oxygen to the blood. It was observed that the volume of gas in the system decreased very quickly while the animal was breathing and immediately after diving, whilst it remained virtually constant during most of the immersion period. The results of one experiment are plotted in Fig. 3. In this graph the time courses of the volume change during the early stages of each breathing-diving sequence are shown, plotted cumulatively throughout the experiment. The air bubble was renewed sometime during the periods represented by the dashed lines when very little volume change was being measured. Also plotted in Fig. 3, again in a cumulative fashion, are the volumes of oxygen removed from and of carbon dioxide added to the gas phase as determined by analysis of the bubbles during renewal. Good agreement was reached between the measurements of volume changes and the values obtained by subtracting lung carbon dioxide output from oxygen uptake (Fig. 3).

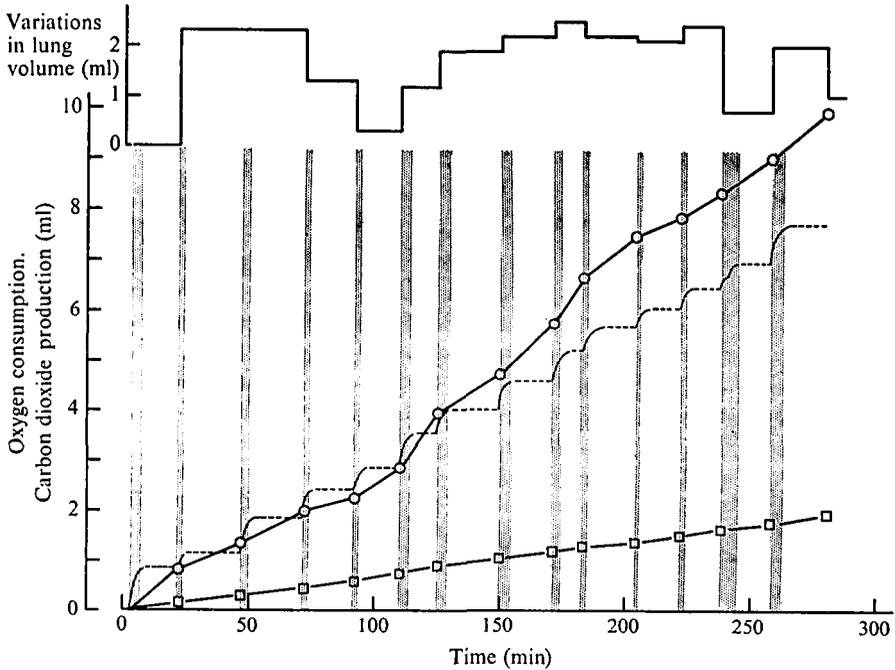


Fig. 3. Aerial oxygen consumption (○) and carbon dioxide production (□) in *Xenopus* (85 g) as measured by the bubble technique. The alternately continuous and broken line plots the measured fall in volume of the lungs as it occurred during each breathing-diving cycle. The plot is shown as a cumulative one throughout the experiment so that comparison with the gas exchange lines is easier. The upper part of the figure shows variation in lung volume at the end of every diving period. The hatched zones represent emergence periods.

This we take to be good evidence that the determinations of volume change give valid estimates of the rate of gas exchange in the lungs. The rate is clearly highest during the breathing period and falls to very low levels only a few minutes after submergence.

(ii) Gas concentrations in blood during breathing and diving periods

Unfortunately the breathing behaviour in animals that had been subjected to surgical procedures was not precisely the same as that seen in intact animals. The former tended to breathe for brief periods at relatively short intervals (3-4 min). Because of the time required for sampling and analysing the blood, the relatively high frequency of breathing did not allow a systematic study of the rates of decrease in oxygen levels during diving, as it was often impossible to take more than one sample in each period.

Simultaneous measurements of the partial pressures of oxygen in systemic and pulmocutaneous blood showed that the values in the former were consistently higher than those in the latter (Fig. 4). The difference was greatest during breathing periods and during a dive the values gradually moved together.

The mean value for the P_{O_2} in systemic blood during breathing periods was 80.4 ± 11.5 mmHg ($n = 116$), but much higher values (between 90 and 110 mmHg) were found occasionally in periods of very active breathing. The corresponding value

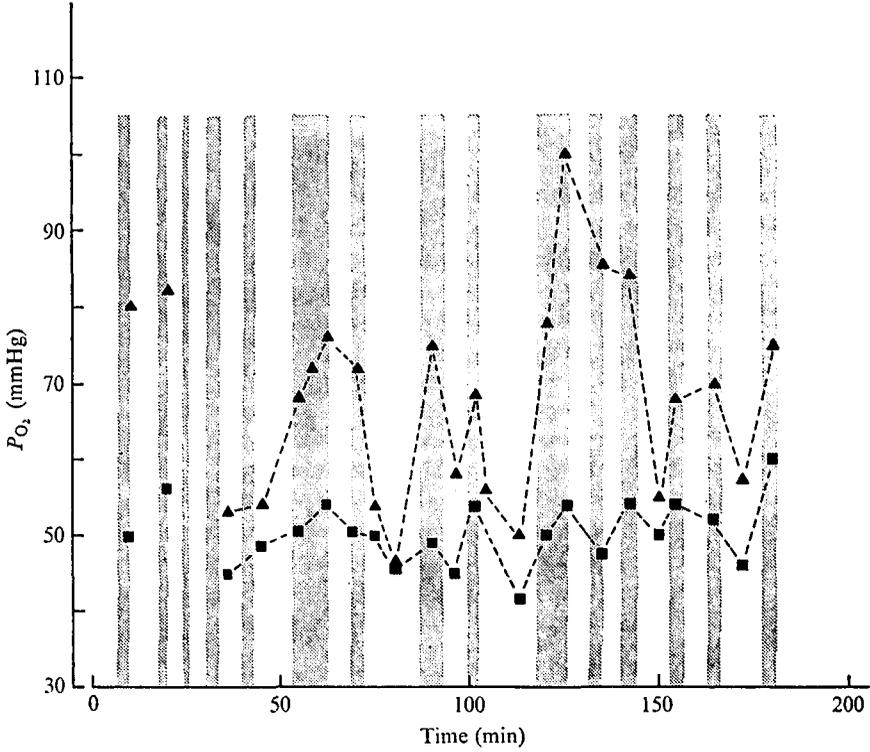


Fig. 4. Partial pressures of oxygen in systemic (▲) and pulmocutaneous (■) arterial blood of *Xenopus* (100 g). The hatched zones represent emergence periods.

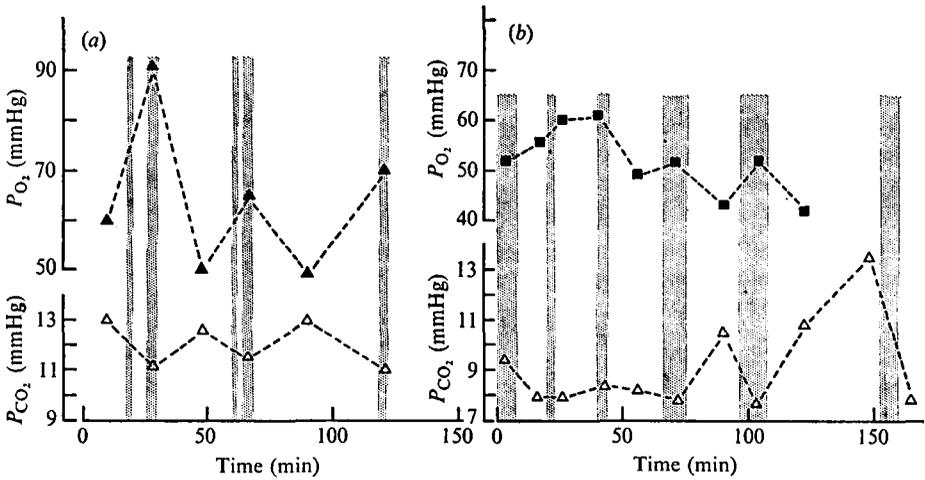


Fig. 5. Partial pressure of oxygen and carbon dioxide in the arterial blood of two *Xenopus*: (a) 100 g, (b) 105 g. ■, Oxygen in pulmocutaneous blood; ▲, oxygen in systemic blood; △, carbon dioxide in systemic blood. The hatched zones represent emergence periods.

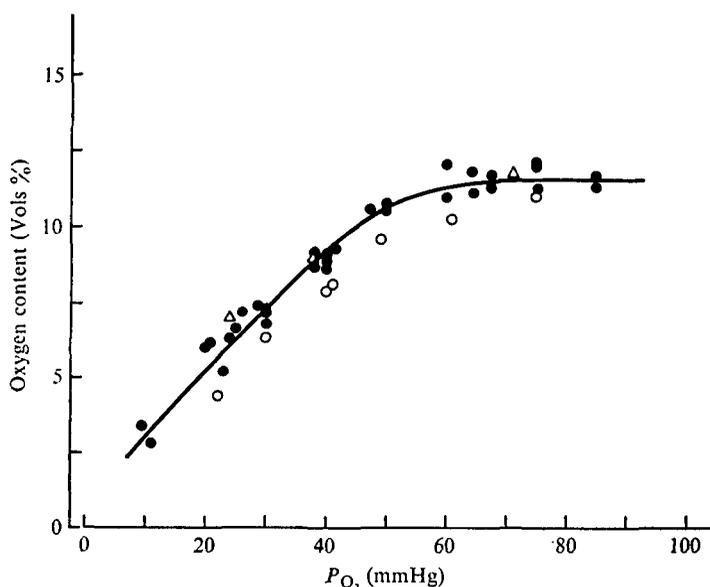


Fig. 6. Oxygen dissociation curve for *Xenopus* blood (20 °C). ●, Samples equilibrated with 9–11 mmHg of CO₂; ○, samples equilibrated with 20 mmHg of CO₂; △, samples equilibrated with 0 mmHg of CO₂.

for pulmocutaneous blood was 60.1 ± 10.0 mmHg ($n = 63$). Two minutes after submergence the mean values were, respectively, 59 mmHg ($n = 8$) and 49 mmHg ($n = 11$). Few samples were obtained after longer periods than this because of short diving periods already discussed. Five determinations in systemic blood taken 4–5 min after diving were between 46 and 62 mmHg. The mean partial pressure of oxygen in the lungs during breathing periods was very high (124 ± 17 mmHg, $n = 35$). It was difficult to obtain lung gas samples during diving periods, probably due to collapse of the tissues around the cannula. In three samples taken approximately 1 min after immersion the values were 80, 100 and 110 mmHg, and in two samples taken after 4 min, 70 and 80 mmHg.

Determinations of the partial pressure of carbon dioxide were carried out on blood of five animals. Simultaneous determinations in both systemic and pulmocutaneous systems were not possible, as only one electrode was available. The values observed in both the systemic and the pulmocutaneous blood were between 13 and 8 mmHg in most cases. Occasionally smaller values were recorded, which were below the measuring capabilities of the instruments. No significant difference was found between systemic and pulmocutaneous blood but there was a fluctuation of values in relation to the breathing rhythm, with lower readings during breathing periods and higher readings during immersion (Fig. 5 *a, b*).

The oxygen dissociation curve obtained from measurements on the blood of eight animals is shown in Fig. 6. The haematocrits of the samples taken varied from 25 to 42% and the points plotted in Fig. 6 show the values for oxygen content after correction to 35% haematocrit in all cases. Full saturation was reached at an oxygen partial pressure of 65 mmHg when the carbon dioxide partial pressure was 10 mmHg. At this

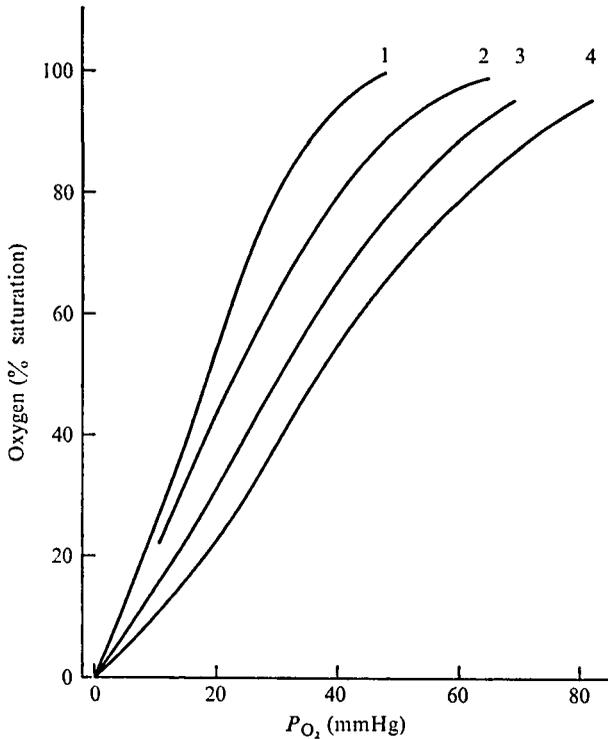


Fig. 7. Comparison of the oxygen dissociation curves of blood from four species of amphibia. Curves 1, 3 and 4 are reproduced from Lenfant & Johansen (1967). 1, *Necturus* (20 °C, P_{CO_2} = 6 mmHg); 2, *Xenopus* (20 °C, P_{CO_2} = 10–12 mmHg); 3, *Amphiuma* (22 °C, P_{CO_2} = 8.5 mmHg); 4, Bullfrog (22 °C, P_{CO_2} = 10 mmHg).

level of carbon dioxide the blood had a pH of 7.50–7.60, and the mean value for total carbon dioxide content was 25 vols %. The oxygen affinity was lower at high partial pressures of CO_2 (20 mmHg) as Fig. 6 shows, but the Bohr effect was not studied in detail.

DISCUSSION

The rate of oxygen uptake from the environment fluctuates over a wide range depending on whether *Xenopus* is breathing at the surface or is submerged. According to our observations about 70% or more of the total oxygen consumption is absorbed through the lungs and the remainder through the skin. This figure is higher than that obtained by Hutchison *et al.* (1968), though their determinations were made with the animal in air which may have increased cutaneous exchange. In fact, Czopek (1955) has suggested that the cutaneous capillary net is rather poorly developed in *Xenopus* compared with other Amphibia. During a dive the diffusion gradient for oxygen over the skin should be increased, since oxygen tension in the pulmocutaneous arch falls more than that in the environment. In addition, Poczopko (1957, 1959) has shown in other anurans that the number of cutaneous capillaries open to blood flow increases during diving or other conditions of respiratory stress. Both of these changes should increase the uptake of oxygen through the skin but their effects were not large enough to be measurable in our experiments. It is worth while to point out that the

significance of an increased number of open skin capillaries in terms of the quantity of oxygen transferred to the blood has not been established, even if the phenomenon does occur in *Xenopus* when diving. Nor is it possible to quantify the change in diffusion gradient since oxygen tension was measured only in the arterial side of the cutaneous circulation. Certainly the variations during a dive were not large in the cutaneous artery and were much smaller than those found in the systemic circulation.

In spite of the substantial fluctuations in the rate of oxygen uptake, storage in lungs and blood may mean that the tissues are not subjected to equivalent variations in their metabolism. It has been suggested that the pulmonary vasoconstriction occurring during a dive is a way of 'metering out' the oxygen contained in the lungs (Shelton, 1970). The fact that more than 80% of the total carbon dioxide produced by the animal is lost via the skin means that there is a fall in volume in the lungs during gas exchange and the evidence shows that this can be used to indicate rate of oxygen uptake. In all the experiments it was clear that after the first 2 or 3 min of a dive gas exchange in the lung dropped to a low and often negligible level. When the animal was breathing at the surface, on the other hand, the rate of exchange was high though rarely at a constant level. It usually declined gradually during the later stages of a period at the surface. These results show quite clearly that pulmonary vasoconstriction is not effective in regulating a more or less uniform oxygen transfer from the lungs throughout a dive. In fact it seems more likely that the stores of oxygen contained in the blood and lungs run down together at a rate which decreases rapidly during the early stages of a dive. During this time the oxygen tension drops in all parts of the system, the largest falls being recorded in systemic circulation and lungs, the smallest in the pulmocutaneous circulation. The data indicate a decreasing average diffusion gradient from alveolar gas to pulmonary capillary. Vasoconstriction in the lungs should also reduce the surface for diffusion and thus the transfer factor of the lungs. The changes in both gradient and transfer factor will lead to decreased oxygen uptake from the alveoli. Experiments have shown that the degree of pulmonary vasoconstriction depends on the time elapsed since the last lung ventilation, the degree of inflation of the lungs, and the oxygen levels in either blood or lungs (Emilio & Shelton, 1972). These observations accord well with the results presented here. Vasoconstriction probably begins just after the last lung ventilations at the surface and then increases progressively during the first few minutes of a dive, accompanied by falling oxygen tensions and a decreasing rate of oxygen transfer from lung to blood and blood to tissues.

The data obtained from blood gas analysis show that tensions continue to fall slowly after gas transfer through the lungs has effectively stopped. The oxygen dissociation curve indicates that *Xenopus* blood has a relatively high affinity for oxygen (Fig. 7), falling between curves obtained by Lenfant & Johansen (1967) for *Necturus* (gill breathing) and *Amphiuma* (lung breathing). The affinity in all three cases is higher than that of the blood of the more terrestrial bullfrog. It is quite clear that the tensions reached in systemic blood when *Xenopus* is breathing are sufficient for complete saturation of the haemoglobin. After a prolonged period of breathing, oxygen tension in the pulmocutaneous artery also rises to a level at which, even with fractionally higher carbon dioxide tensions to be expected in mainly venous blood, the haemoglobin is 90% saturated. Around this level the animal usually stops breathing and

dives, whereupon the oxygen tension of blood in both systemic and pulmocutaneous circulations drops rapidly to levels on the steep part of the dissociation curve, where tension changes have the maximum effect on oxygen content. The difference in oxygen tension between the two sides of the circulation decreases during a dive, becoming very small after 20–30 min. At the end of a dive of this duration, the oxygen tensions indicate that the blood is approximately 50% saturated with oxygen. Thus, assuming a blood volume of 8 ml for a 100 g *Xenopus* (Jones, 1972), a maximum of 0.5 ml O₂ would be released from the blood to the tissues between the time that the toad stopped breathing and dived and the time of the next lung ventilations. Some 30% of this would be transferred after vasoconstriction had reduced the lung contribution to unmeasurable levels. Taking the stores of oxygen and the skin exchange into account, it is unlikely that the total consumption by the tissues during a dive of average duration could amount to as much as one half the overall rate of oxygen consumption. Some modifications of metabolism must be called for, as Jones (1972) has suggested. Recovery of the oxygen levels to the point where the haemoglobin is fully saturated is achieved after some three or more minutes spent ventilating the lungs at the surface. It is, in part, responsible for the high rate of oxygen transfer from the lungs during this period. Further breathing movements increase the oxygen tension in both lungs and arterial blood to levels greatly in excess of that needed for full saturation.

The simultaneous determination of oxygen tensions in the systemic and pulmocutaneous circulations reveals that, in a breathing animal, quite substantial differences exist between the oxygen tensions of the blood on the two sides. These results add to the convincing body of evidence which supports the hypothesis that there is selective distribution of blood coming from right and left atria through the single ventricle. During a dive the differences become less marked and clearly the haemodynamic properties of the system must change as blood flow in the lung circuit is greatly reduced. Whether there is still selective distribution when the stroke volumes of the two atria are so different is not easy to determine using the evidence from blood gas concentrations. A complete analysis of this long-standing problem of blood distribution and the related haemodynamic mechanisms in the undivided amphibian heart is still not possible.

Another fundamental problem in these animals is that of control of metabolism and gas exchange. The importance of oxygen availability in relationship to metabolic rate is discussed by Jones (1972) but the mechanisms which regulate oxygen availability are still difficult to understand. The experiments show that lung ventilation is by far the most significant activity affecting gas exchange and the levels of oxygen and carbon dioxide in lungs and blood. They also show that lung volume, rate of gas exchange, and gas concentrations in lungs and blood, vary over a considerable range. None of the variables seems to act in a simple way in controlling the beginning, the intensity, and the end of a period of lung ventilation. The limits reached vary considerably from cycle to cycle. It is likely that, as in the case of pulmonary vasoconstriction (Emilio & Shelton, 1972), many of the variables combine in a complex manner to become the effective signals responsible for starting and stopping lung ventilation.

SUMMARY

1. Unrestrained *Xenopus* with access to air had an oxygen consumption, as measured at 20 °C by manometric and electrode techniques, of approximately 4.5 ml O₂ 100 g⁻¹ h⁻¹ of which 1.1 ml was taken in through the skin.

2. Measurements of body volume showed that the rate of oxygen uptake from the lungs was high when the animal was at the surface but fell rapidly during the first few minutes of a dive.

3. Oxygen tensions in systemic (80 mmHg) and pulmocutaneous (60 mmHg) vessels provided evidence for separation of blood flows in the ventricle of the animal when breathing air. The tensions fell in all parts of the circulation throughout a dive.

4. The above data, together with a conventionally determined oxygen dissociation curve, show that both blood and lungs are used to a limited extent as oxygen stores during a dive, the blood being more important. The stores do not permit tissue consumption to go on at a uniform rate throughout a normal breathing – diving cycle.

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