

14 Human Respiratory Adaptations for Swimming and Diving

John M. Patrick

SUMMARY

This chapter reviews those features of the human respiratory system that might represent adaptations beneficial for hominids spending appreciable periods of their lives in shallow water. Large static lung volumes provide buoyancy, but the ability to increase mean lung volume by voluntary breathing control (together with the relatively high body fat content) seems much more valuable in this regard. Several reflexes help to keep water out of the airway by causing broncho-constriction or by reducing ventilatory drive, but these are rather weak in *Homo sapiens*. The pattern of breathing utilised for human speech is also the pattern that provides the greatest mean buoyancy and the least chance of inhaling water. The ability to switch to this pattern has required the development of voluntary breathing-control. No conclusive evidence is available to link the respiratory characteristics of modern *Homo* with those that might have provided selective advantages to earlier hominids living in an aquatic habitat. However, the ability to control breathing from the cerebral cortex rather than from the brain stem could be regarded as a respiratory adaptation suiting hominids to life in shallow water.

INTRODUCTION

In the three published reviews of the Aquatic Ape Theory (Hardy, 1960; Morgan, 1982; Verhaegen, 1985), it has been suggested that there are several adaptations in the respiratory system that contribute to the ability of humans to survive in water. These are:

- (a) the respiratory and metabolic components of the so-called 'diving reflex' (cf. Scholander, 1966);
- (b) the anatomical and physiological features of the nose and nasopharynx (Morgan, 1982; Verhaegen, 1985); and above all:
- (c) the ability to switch the control of breathing from an automatic to a voluntary mechanism (cf. Phillipson *et al.*, 1978). Morgan has also drawn a striking evolutionary parallel between this voluntary type of breathing control, which is required for living in water, and the breathing control required for the production of speech.

Although these respiratory adaptations have not been emphasised, they would have been of vital importance for an aquatic ape, because periods of submergence inevitably occur during wading, paddling, floating, swimming or diving; and even the shortest submersion entails a

disturbance of normal respiratory function. So these and other possible respiratory adaptations demand specific discussion when the merits of this controversial evolutionary hypothesis are being considered.

We shall not need to concern ourselves here with diving physiology proper, nor consider the acute effects on the human body of the hydrostatic pressure of great depths. At 100 m the total pressure is 11 atmospheres, and the chest is squeezed to 10 per cent of its volume on the surface. Nevertheless, unassisted 'free' or 'skin' dives to this depth have been recorded: the breath can be held for about 5 minutes on submergence during a deep dive; and commercial diving to a depth of 25 m is common in the Yellow Sea off Korea and Japan. However, the evolutionary selection pressures that we need to consider are those promoting the ability to work and play in relatively shallow water, and certainly not far below the surface. So the term 'dive' in this chapter is simply synonymous with 'going under water'.

We can confine our discussion, therefore, to those features of the human respiratory system that (1) provide buoyancy, (2) keep water out of the airway, and (3) allow short periods of submergence. The first two are straightforward: any small variation that tends to keep the airway opening up out of the water or tends to prevent water from entering the airway would seem to offer a selective advantage in an aquatic environment. However, the evolution of the ability to 'dive' demands a compromise between conflicting requirements. On the one hand, safety requires not only a clear physiological signalling to the diver of the developing asphyxia but also a quick recovery on resurfacing. On the other hand, productivity while hunting for food or treasure below the surface depends upon the ability to prolong the dive. The former criterion is met by brisk responses to hypoxia and hypercapnia, and the latter by blunted ones. Arguments for or against adaptation to an aquatic environment that are based on breath-holding ability may therefore be two-edged.

LUNG SIZE AND BUOYANCY

During the evolution of aerial respiration in aquatic vertebrates, the buoyancy provided by the air in the lungs would have been just as important as the facility for gas exchange, because it would have helped to keep the animal on the surface (Wind, 1976). Much more recently, the readaptation of primates to an aqueous environment would again have been facilitated by having a buoyant body mass. Buoyancy would have been advantageous for life in shallow water long before any adaptations that permit 'diving' would have had a chance to prove beneficial. To stay on the surface, the density of the body has to be less than that of the water we float in, and the difference has to be great enough to keep not just the top of the head but the airway opening itself

above the surface. The colder and saltier the water is, the more dense it is, and therefore the easier it is for a given object to float. So if ancestral hominids went through an aquatic phase in tropical fresh waters, they would have required considerable buoyancy aids; less so if they were living in tropical seas, but still more than we need now when we bathe in the North Atlantic.

There are no systematic studies of the factors contributing to primate buoyancy (see Wind, 1976), but my impression is that lung volume is a less important contributory factor than body fat. For example, in a warm freshwater swimming-pool, I float head-up with my mouth and nose well above the surface when I hold my breath with my lungs fully inflated. But when my sons do the same, they sink to the bottom. They are as tall and as large-lunged as I am, but they are not so fat; and I only have to exhale about half my vital capacity before my body density rises to unity and my mouth and nose sink irretrievably below the surface. Tenney and Remmers (1963) compared lung sizes among species across a wide range of sizes, and showed that some but not all marine species have a slightly greater lung volume than terrestrial species with the same body mass (Kooyman, 1973). Nevertheless, men have larger lung volumes than women (after allowing for body size), and it is possible that this sex difference may have evolved during an aquatic phase as an adaptive compensation for men's relative deficiency of fat deposits. In addition, the study by Lane and Mitchem (1963) suggested an ethnic factor in buoyancy: 10 per cent of their white subjects, but 70 per cent of their black subjects, sank when they assumed a curled posture in water after a full inspiration. Ghesquiere and Bunkens (this volume, chapter 16), show theoretically that black subjects might be less buoyant than whites. This needs direct confirmation, because there are ethnic differences in lung size at a given stature, with blacks having the smaller lungs (Patrick, 1988).

Dobeln and Holmer (1974) showed that the measured sinking force was proportional to the body weight in water, and was positive even for the lightest of their fifteen white subjects; that is, they all tended to sink and therefore submerge the airway opening. So they had to expend energy in treading water, in order to keep the airway clear of the surface. However, the body's weight in water was reduced by 8.2 N for every extra litre of air inspired, and this made a substantial contribution to the energy saving. The greater the average lung volume (or respiratory mean level) over a period encompassing several breaths, the greater was the saving of energy. So the best strategy for fat and thin persons alike, black and white, male and female, irrespective of the initial lung volume, is to breathe high up in the chest and to have fast then prolonged inspirations (Kooyman, 1973). This can be achieved by voluntary control of breathing, and we shall return to this important topic later.

TR 63
K 73
L+M 63
D+H 74

KEEPING WATER OUT OF THE AIRWAY

Besides buoyancy, a second requirement for survival in an aquatic environment would be the ability to prevent water from splashing or pouring into the airway. For example, the nostrils of seals and other diving mammals are normally closed off, and require muscular action to open them again on emergence from water. The human nasal musculature cannot close the nostrils, and its evolutionary origins could equally well have been the result of selection favouring a range of facial expressions. The oral breathing-route, which can be closed off, is a secondary one which comes into use during and after infancy. To be sure, the soft palate can be lifted to occlude the naso-pharynx and thus prevent the influx of water, but this mechanism is primarily utilised during swallowing, to allow food and liquid from the mouth to cross the airway into the oesophagus, and it has apparently evolved independently of any aquatic phase.

It has been argued by Morgan (1982) that the downward-pointing shape of the human nose might have evolved for the same reason that children hold their noses when jumping head-first into water: to prevent the penetration of water into the sinuses during diving. Certainly it is easier to submerge with the nose pinched off, but an equally plausible terrestrial explanation is that this shape is to direct the circulation of inspired air to the olfactory mucosa, which lies superiorly, to promote the sense of smell; and also to prevent cold, unhumidified and unfiltered air from reaching the openings into the sinuses (Proetz, 1953).

It has also been suggested (Verhaegen, 1985) that an equivalent in humans to the nose-closing of seals is the cyclical or externally triggered nasal obstruction effected by swelling of the nasal mucosa. Verhaegen stated that the nasal resistance oscillates with a period of about 90 seconds, pointing out that this corresponds with the interval between dives in the Ama of Korea and Japan. There are at least two problems with this hypothesis: (1) the period is 2–3 hours rather than 90 seconds, and the total nasal resistance is barely changed by the oscillation, which alternates between the two sides (Principato and Ozenburger, 1970); and (2) the resistance is not raised but lowered by two important consequences of diving: (a) the exercise and (b) the raised carbon dioxide pressures (Dallimore and Eccles, 1977).

Nevertheless, mammals have many reflexes which help to protect the airway as a whole against penetration by droplets, particles or irritant vapours. These reflexes differ widely between species, and have been extensively reviewed by Widdicombe (1986). Broadly speaking, there are receptors on the face, in the nose and the upper airway, on the larynx and in the larger bronchioles, and these are triggered by a variety of stimuli. There is also a variety of responses, but the ones that are relevant

here are those tending to close the airway (at the level of the soft palate, the larynx or the bronchioles), and also those tending to reduce or inhibit breathing movements. There have been rather few studies of these reflexes in human subjects, so much of the evidence comes from animal experiments indicating many species differences, some of which are between 'diving' and 'terrestrial' mammals.

These protective reflexes can be triggered in human subjects as well as in many other mammals by the application of water to the area of the face around the mouth and nose, and they are accompanied by a reduction in heart rate and by other cardiovascular and metabolic changes. These together protect the heart and brain from hypoxia, by reducing the rate of oxygen consumption and redistributing the blood-flow away from less vital organs. This combination of responses is termed the 'diving reflex', and has recently been thoroughly reviewed by Elsner and Gooden (1983) and by Daly (1984). These diving responses can be studied relatively simply in the laboratory, without the need for submergence: only the face need be wetted.

We have studied the bronchomotor response to face immersion in ten normal male subjects (Mukhtar and Patrick, 1984), and measured the maximum airflow during a forced expiration at two different lung volumes: this gives an index of the diameter of the small airways. The subjects immersed their faces in cold fresh water at 10°C for 15 seconds, and half of them showed a significant bronchial narrowing. The extent of the broncho-constriction, however, was only about 14 per cent. Similar findings have been reported by Josenhans, Melville and Ulmer (1969), and a slightly greater effect was seen by Keatinge and Nadel (1965) when their subjects took ice-cold showers but kept their faces dry. This sort of reflex would be advantageous to an aquatic hominid; but, again, it would be more so if it were greater in magnitude and if it were triggered by warmer water too. It appears to offer little protection to the respiratory tract now.

If the airway does not close to prevent the entry of water, perhaps respiratory movements might be stopped instead. The reflex apnoea seen in diving mammals when they submerge is remarkable. Daly, Elsner and Angell-James (1977) have studied the harbour seal, anaesthetised but able to breathe through a tracheostomy tube. When a face-mask filled with water at 20°C was applied to the snout, the seal stopped breathing at once and exhibited a profound bradycardia too. Surprisingly, this diving response is not confined to diving mammals, but is also seen in rabbits and in sheep and lambs (Tchobroutsky, Merlet and Rey, 1969). When water touches the larynx of new-born dogs, breathing stops for a while, but as the puppies get older the reflex gradually disappears (Boggs and Bartlett, 1973). Curiously, salt water does not have the same effect. This type of reflex probably occurs in human neonates, who apparently can

safely be born under water. It would be advantageous for adult aquatic apes only if it persisted into adulthood, and if sea water were equally effective in triggering it.

We have repeated Daly's harbour seal experiment in conscious young men breathing through a respiratory valve mounted in the bottom of a bowl of water (Mukhtar and Patrick, 1986). When cold water is flooded onto the face of human subjects breathing air or carbon dioxide, either at rest or in exercise, there is at most a small fall in ventilation which comes on slowly with a time course that appears to parallel the change in face temperature. We showed that the response was not due to anxiety, to airway cooling or to brain cooling: it appears to be due to the cooling of the face. Folgering and Olivier (1985) found a somewhat greater effect in resting subjects with cold ice-packs. So here is another possible adaptive response that would be of advantage to an aquatic hominid, but again it is slow in onset, small in extent, and not triggered by immersion in warmer water.

So far the evidence for human respiratory adaptations that would facilitate living in an aquatic habitat appears rather meagre. First, lung volumes do not seem adapted to provide much extra buoyancy. Second, the nose and nasopharynx do not close the airway off to any useful extent, and their shapes are not uniquely designed for protection against water entry. And third, the respiratory diving reflex that is triggered by water on the adult face causes no more than a 15 per cent reduction in airway diameter and a 15 per cent reduction in the respiratory centre's drive to breathe. Furthermore, it is slow in onset and ineffective in warm water. Nevertheless, there remains another mechanism in humans that can both contribute to buoyancy and effectively seal off the airway. This extremely powerful mechanism is the cortical control of breathing.

CORTICAL CONTROL OF BREATHING

For most of the time our breathing is under automatic control from 'low' (that is, brain-stem) centres: this provides a ventilation volume appropriate to the requirements for normal metabolic gas exchange. But there are times when we need to use the chest and lungs to generate truncal pressures for straining and for lifting loads, and for blowing and phonation. For these, the mechanism is switched to a cortical controller, and a variety of motor programmes is available. Patterns of breathing very different from the automatic one are seen, and the switch between the two is extremely rapid (Phillipson *et al.*, 1978). During speech, the inspirations are short and steep and the expirations long and slow in order to provide low airflow rates for phonation. Quite apart from its importance for communication (Morgan, 1982), the ability to produce this 'phonatory breathing pattern' would have two advantages for the

aquatic ape: it would permit efficient swimming and it would promote buoyancy.

It is technically difficult to study breathing patterns during natural swimming, because the use of any snorkel-like equipment alters the spontaneous pattern. But the anecdotal evidence is that the pattern which does occur resembles that during phonation on land. Holmer (1972) reports that 'respiration in swimming is influenced by stroke rhythm and water pressure. Rapid inspiration is followed by slower expiration under water'. The respiratory movements have to be entrained or synchronised with the limb movements, because the head and trunk move up and down through the surface with each stroke. Respiratory patterns are not entrained with limb movements during laboratory cycle-ergometer or treadmill exercise in naïve subjects (Kay, Petersen and Vjeby-Christensen, 1975); so the evolution of this mechanism of voluntary control which enables speech to occur is particularly suitable for swimming. Non-automatic respiratory control while swimming can provide buoyancy too. Dobeln and Holmer (1974) showed that by voluntarily adopting a breathing pattern similar to that of phonation on land, the mean lung volume during the respiratory cycle is increased and the average sinking force can be reduced by 10 per cent, thus reducing the metabolic cost of paddling to keep afloat by about 150 ml O₂ per minute. The reflex inspiratory gasp (Keatinge and Nadel, 1965) that occurs when the body is immersed head-out in cold water also contributes to buoyancy.

The second example of cortical respiratory control relevant to swimming and diving is voluntary breath-holding. We all know from our own experience that we can hold our breath for about a minute, and that this period can be extended by holding with a full chest and also by over-ventilating to blow off some carbon dioxide beforehand. Japanese macaques have also been observed holding their breath when preparing to dive. The consequences of the cessation of effective gas exchange ultimately compel the automatic medullary mechanisms to take control again and restart respiratory movements at the breaking-point. For safe diving, it is clearly important that timely warning of the impending breaking-point is sensed, so that the diver can return to the surface and avoid inhaling water. The carbon dioxide drive contributes to this warning, and if carbon dioxide is blown off too vigorously in a pre-dive hyperventilation, the hypoxia that is induced by the underwater exercise during breath-holding may lead to unconsciousness and drowning (Craig and Babcock, 1962).

For prolonged productive diving we might expect to see adaptations that delay the onset of the breaking-point. One possible mechanism would be for the control system to become less sensitive to the asphyxial stimuli, and this is what happens in the seal (Daly, Elsner and Angell-

James, 1977). An aquatic ape might be expected to have possessed a similar respiratory diving reflex. The evidence from human subjects is somewhat conflicting, but it provides no suggestion that respiratory drive during submersion is profoundly reduced like the seal's. We have already seen that the fall in ventilation on human face immersion is small. Mukhtar and Patrick (1986) also measured maximum breath-holding times when the subjects' faces were in air (56 seconds), in cold water (66 seconds), and in warm water (56 seconds): that is, cold face immersion only modestly enhances breath-holding abilities. Hayward *et al.* (1984) have done the experiment differently, pitching their subjects bodily into a pool at different temperatures. By contrast, they found that the maximum submersion times fell from 45 seconds at 35°C to 15 seconds at 0°C. Sudden immersion of the whole body in cold water thus reduces breath-hold times, perhaps because of the reflex inspiratory drive described by Keatinge and Nadel (1965). Overall, the reflex effect of face immersion on ventilatory control is small.

CONCLUSION

My conclusion, therefore, is that the only respiratory adaptation that might be of any importance in promoting human survival in an aquatic environment is our capacity for cortical control of breathing. This enables us to time the respiratory cycle appropriately in relation to our paddling or swimming movements, so that we can keep the face out of water long enough to take an inspiration safely. If we submerge, voluntarily or not, we can hold our breath for a minute or so, and longer if we have first taken a full inspiration. Nevertheless, it is not possible to argue convincingly that this mechanism evolved as an adaptation to an aquatic environment; also, it provides obvious selective advantages in terrestrial environments. It enables us to use the chest to control abdominal and pelvic pressures for straining and lifting, and to control thoracic pressures for the production of speech – and for blowing one's own trumpet.

REFERENCES

- Boggs, D.E. and Bartlett, D., 1973, Chemical specificity of a laryngeal apnoeic reflex in puppies. *Journal of Applied Physiology*, **53**, 455–62.
- Craig, A.B. and Babcock, S.A., 1962, Alveolar PCO₂ during breath-holding and exercise. *Journal of Applied Physiology*, **17**, 874–8.
- Dallimore, N.S. and Eccles, R., 1977, Changes in human nasal resistance associated with exercise, hyperventilation and rebreathing. *Acta Otolaryngologica*, **84**, 416–21.
- Daly, M. de B., 1984, Breath-hold diving: mechanisms of cardiovascular adjustments in the mammal. In *Recent Advances in Physiology*, no. 10, (London: Arnold), 201–45.
- Daly, M. de B., Elsner, R. and Angell-James, J. E., 1977, Cardiorespiratory control by carotid chemoreceptors during experimental dives in the seal. *American Journal of*

- Physiology*, **232**, H508-16.
- Dobeln, W. von and Holmer, I., 1974, Body composition, sinking force, and oxygen uptake of man treading water. *Journal of Applied Physiology*, **37**, 55-9.
- Elsner, R., Angell-James, J.E. and Daly, M. de B., 1977, Carotid body chemoreceptor reflexes and their interactions in the seal. *American Journal of Physiology*, **232**, H517-25.
- Elsner, R. and Gooden, B.A., 1983, *Diving and Asphyxia*. Monographs of the Physiological Society, Cambridge, no. 40.
- Folgering, H. and Olivier, O., 1985, The diving response depresses ventilation in man. *Bulletin européen de Physiopathologie Respiratoire*, **21**, 143-7.
- Ghesquiere, J. and Bunkens, H., 1991, The burden of locomotion in water: could the aquatic ape have overcome it? (This volume, chapter 16.)
- Hardy, A., 1960, Was man more aquatic in the past? *New Scientist*, **7**, 642-5.
- Hayward, J.S., Hay, C., Matthews, B.R., Overweel, C.H. and Radford, D.D., 1984, Temperature effect on the human dive response in relation to cold-water near-drowning. *Journal of Applied Physiology*, **56**, 202-6.
- Holmer, I., 1972, Oxygen uptake during swimming in man. *Journal of Applied Physiology*, **33**, 502-9.
- Josenhans, W.T., Melville, G.N., Ulmer, W.T., 1969, The effect of cold facial stimulation on airway conductance in healthy man. *Canadian Journal of Physiology and Pharmacology*, **47**, 453-7.
- Kay, J.D.S., Petersen, E.S. and Vjeby-Christensen, H., 1975, Mean and breath-by-breath pattern of breathing in man during steady-state exercise. *Journal of Physiology*, **251**, 657-69.
- Keatinge, W.R. and Nadel, J.A., 1965, Immediate respiratory response to sudden cooling of the skin. *Journal of Applied Physiology*, **20**, 65-9.
- Kooyman, G.L., 1973, Respiratory adaptations in marine mammals. *American Zoologist*, **13**, 457-68.
- Lane, E.C. and Mitchem, J.C., 1963, Buoyancy as predicted by certain anthropometric measurements. *Research Quarterly*, **35**, 21-8.
- Morgan, E., 1982, *The Aquatic Ape* (London: Souvenir Press).
- Mukhtar, M.R. and Patrick, J.M., 1984, Bronchoconstriction: a component of the 'diving response' in man. *European Journal of Applied Physiology*, **53**, 155-8.
- Mukhtar, M.R. and Patrick, J.M., 1986, Ventilatory drive during face immersion in man. *Journal of Physiology*, **370**, 13-24.
- Patrick, J.M., 1988, Ventilatory capacity in tropical populations: constitutional and environmental influences. *Proceedings of the IUBS/SSHB Symposium on Working Capacity in Tropical Populations, 1984*. (Cambridge: Cambridge University Press), 31-50.
- Phillipson, E.A., McClean, P.A., Sullivan, C.E. and Zamel, M., 1978, Interaction of metabolic and behavioural respiratory control during hypercapnia and speech. *American Review of Respiratory Disease*, **117**, 903-9.
- Principato, J.J., and Ozenburger, J.M., 1970, Cyclical changes in nasal resistance. *Archives of Otolaryngology*, **91**, 71-7.
- Proetz, A.W., 1953, *Applied Physiology of the Nose*, 2nd edn. (St Louis: Mosby).
- Scholander, P.F., 1966, The master switch of life. *Scientific American*, **209** (6), 92-9.
- Tchobroutsky, C., Merlet, C. and Rey, P., 1969, The diving reflex in rabbit, sheep and newborn lamb and its afferent pathway. *Respiration Physiology*, **8**, 108-17.
- Tenney, S.M. and Remmers, J.E., 1963, Comparative quantitative morphology of the mammalian lung: diffusing area. *Nature*, **197**, 54-6.
- Verhaegen, M.J.B., 1985, The aquatic ape theory: evidence and a possible scenario. *Medical Hypotheses*, **16**, 17-32.
- Widdicombe, J., 1986, Reflexes from the upper respiratory tract. In *Handbook of*

Physiology. 3: The Respiratory System. vol II: Control of breathing (The American Physiological Society), 363–94.

Wind, J., 1976, Human drowning: phylogenetic origin. *Journal of Human Evolution*, 5, 349–63.