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Evolutionary Trends in Respiratory Mechanisms

William K. Milsom

Abstract As we progress through the vertebrate phyla we see a number of changes in the functional morphology of the respiratory system that offer insights into the physiological systems that control them. We see a switch from a buccal pump powered by branchiomic and hypobranchial muscles innervated by cranial nerves to a thoraco-abdominal aspiration pump powered by axial muscles innervated by spinal nerves with pre-motor neurons situated in the ventral respiratory column. The initial steps in the evolution of air breathing were a behavioural commitment to surface and changes in valving of the mouth/spiracle/nares and the operculum and glottis (or their equivalents) (*i.e.*, changes in the activation of the muscles dilating and/or constricting various openings). These allowed the production of water breaths versus deflation or inflation of the air-breathing organ. Changes in the respiratory pump muscles evolved later. While highly speculative, it is suggested that these three independent valving circuits may have arisen in association with different pairs of segmental rhythm generators, and that all circuits continue to work together in a coordinated fashion to produce all types of breaths (including eupneic breaths and gasps).

1 Introduction

The evolution of respiratory mechanisms in vertebrates progresses from aquatic ventilation primarily driven by a buccal force pump to aerial ventilation primarily driven by an aspiration or suction pump. Bearing in mind that there are numerous variations in the mechanisms that underlie the operation of these pumps, several general trends can be recognized. The first is a switch in the primary muscle groups associated with these two pumps. The buccal force pump operates with branchiomic and hypobranchial muscles associated with the buccal and pharyngeal cavities. These muscles are innervated by cranial nerves, specifically the trigeminal, facial and hypoglossal nerves. The aspiration pump is driven primarily by axial muscles associated with the thorax and abdomen and innervated by spinal nerves.

University of British Columbia, Department of Zoology, milsom@zoology.ubc.ca

These nerves receive excitation primarily from pre-motor neurons in the ventral medullary respiratory column. A muscular diaphragm is found only in mammals but is none-the-less of axial origin and innervated by spinal motor neurons. Many ideas have been put forward concerning the origins of aspiration breathing (Brainerd, E.L. 1999; Brainerd and Owerkowicz 2006) and the mammalian diaphragm (Perry, Codd and Klein 2005), which are beyond the scope of this brief review. The focus of this review will be on how changes in respiratory mechanics and behaviour, particularly associated with the advent of air-breathing (via buccal force pump and aspiration suction pump) alter the phase relationships of the various pumps and the implication of this for the evolution of respiratory central rhythm generators.

2 Pulmonary Mechanics, Behaviour and the Phases of the Respiratory Cycle

2.1 *Water Breathers*

In adult lampreys, branchial muscles surround the branchial basket, which consists of elastic cartilage and contains the gill sacs. Synchronous contraction of these muscles compresses the branchial basket and produces exhalation. As the muscles relax, the spring-like basket expands by passive recoil drawing fresh water back into the sacs. Ventilation is often tidal, in and out through the pharyngeal gill slits. In larval lampreys and in hagfish, ventilation is unidirectional. The branchial muscles contract during exhalation just as in the adults. Unlike in adults, the valves over the gill openings close during branchial expansion so that water is drawn in through the mouth. Larvae also use the velum (a pair of muscular pouches in the pharynx) to push water from the pharynx during exhalation (Fig. 1) (Johansen and Strahn 1963).

In all of the remaining water-breathing vertebrates, both phases of the buccal ventilation cycle are active. While a second pump operates outside the gills to expand and compress the parabronchial or opercular cavity, it is the buccal pump that primarily powers ventilation. Water flow is uni-directional, in through the mouth/ spiracle/nares (depending on species) and out over the gills (Fig. 1) (Shelton 1970).

2.2 *Early Air Breathers*

The origins of air breathing were initially associated with a behavioural commitment to swim to the surface of the water and changes in valving of the mouth/spiracle/nares and the operculum and glottis (or their equivalents). At least 47 species from 24 genera of bony fish are known to breathe air using a lung or a respiratory gas bladder. These fishes use the same buccal pump that they do for water breathing but devote one full cycle of the pump to each of lung deflation and inflation.

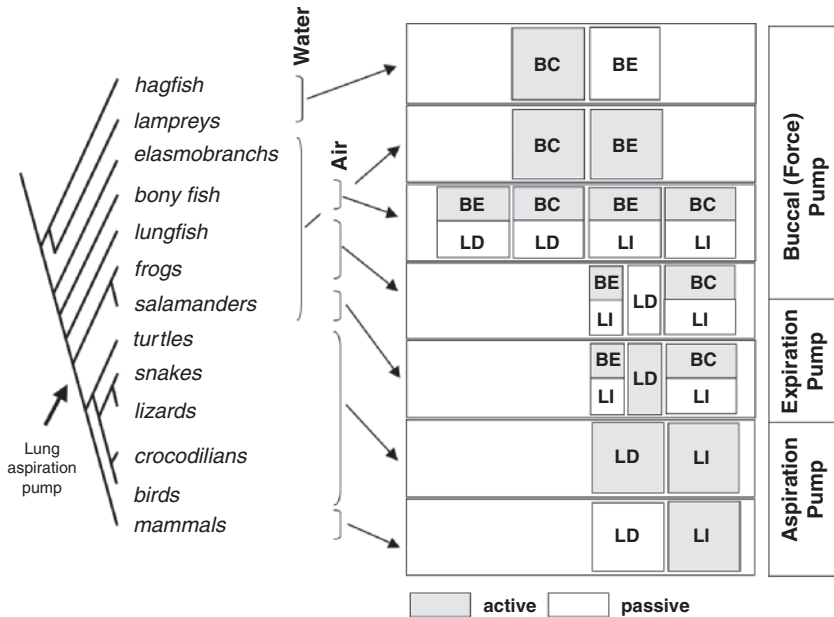


Fig. 1 Dendrogram of various vertebrate groups showing active/passive phases of the buccal/lung ventilation cycles associated with aquatic and aerial respiration. See text for details. (BE = buccal expansion, BC = buccal compression, LD = lung deflation, LI = lung inflation)

The respiratory pause in the lung ventilation cycle is at end-inspiration with the lungs full (Brainerd 1994). What determines whether a cycle of the pump produces a water breath, lung deflation or lung inflation is the valving mechanism that is employed, which orifices are open and which are closed. Without going into detail, the glottis (or sphincter to the air breathing organ) remains closed during a water breath while the glottis remains open but the operculum remains closed during an air breath. Furthermore, the sequence of opening and closing the mouth and glottis are reversed during the buccal expansion and compression phases associated with lung deflation and inflation. The critical point is that three different neural circuits associated with the timing of the opening and closing of the various valves (mouth/spiracle/nares/ operculum/glottis) must exist.

Unlike the bony fishes, in the lungfish and most frogs and toads, both lung deflation and inflation are accommodated within a single buccal pump cycle. Lung deflation is purely passive and occurs during a pause in the buccal cycle (between buccal expansion and compression). Both phases of the buccal cycle are associated with lung inflation; buccal expansion primes the pump by filling the buccal cavity initially and then, following lung deflation, buccal compression is used to force this air into the lung (Vitalis and Shelton 1990). Again, what determines whether a cycle of the pump produces a water breath (in lungfish and anuran larvae; a buccal oscillation in anuran adults), lung deflation or lung inflation is the valving mechanism that is employed. Three neural circuits associated with the timing of the

opening and closing of the various valves (mouth/spiracle/nares/operculum/glottis) must exist here also.

2.3 Active Expiration and the Origins of Aspiration Breathing

Until recently there was no evidence of an intermediate mechanism between the buccal pump of fishes and amphibians and the aspiration pump of reptiles, birds and mammals. It has now been shown, however, that many amphibians use axial muscles for active expiration along with the buccal pump for active inspiration (see Brainerd 1999; Brainerd and Owerkowicz 2006, for reviews). This suggests that aspiration breathing evolved in two steps: (1) from buccal pumping alone to buccal pumping for inspiration and axial muscles for expiration and then (2) to aspiration breathing alone using axial muscles for both expiration and inspiration (Brainerd 1999).

2.4 Aspiration Breathing in “Higher” Vertebrates

Although aspiration breathing consists of both active lung deflation and inflation in reptiles and birds, active deflation is only associated with increased respiratory drive in mammals. Interestingly, in mammals we see a switch in relative contributions of chest wall compliance and air flow resistance to pulmonary work (the former dominates in birds and reptiles, the latter takes on increased importance in mammals), the evolution of a muscular diaphragm and a reduction in the need for active lung deflation as the system returns to functional residual capacity following inhalation.

3 Implications for Central Rhythm Generation

Initially, in water breathing vertebrates, there was one set of pump muscles (those associated with the buccal pump) and one valving mechanism. With the advent of air breathing, multiple valving mechanisms for different behaviours evolved; independent circuits arose for generating a H₂O breath (or buccal oscillation), lung deflation, and lung inflation. While highly speculative, it is possible that the three independent valving circuits may have arisen in association with different pairs of segmental rhythm generators in a rostral-caudal arrangement (Fig. 2). The suggestion put forward in Fig. 2 separates the lung oscillator into a deflation and an inflation oscillator associated with the parafacial respiratory group and the PreBötzinger Complex, respectively, in mammals and implies that none of the oscillators arose anew but all are based on reconfiguring pre-existing embryonic segmental rhythm generators.

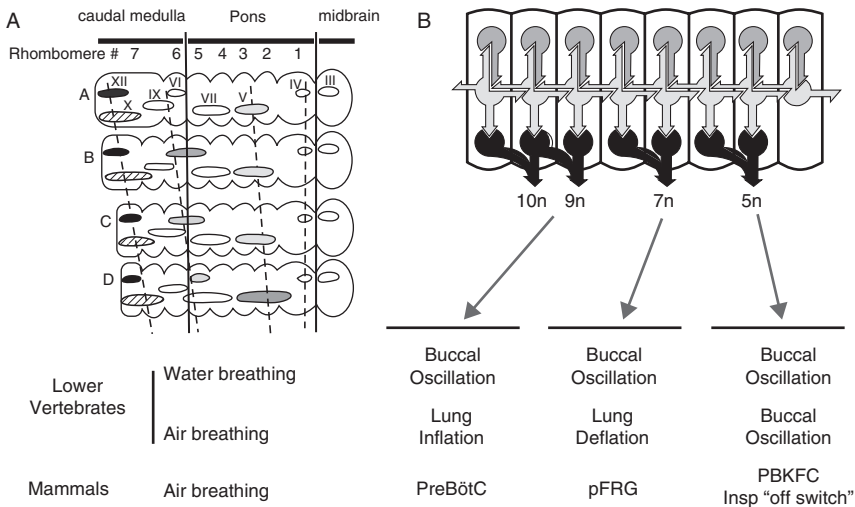


Fig. 2 (A) Hypothetical arrangement of rhythm generators (top), interneurons (middle) and motor neurons (bottom) within the segmented hindbrain of a vertebrate embryo (modified from Champagnat and Fortin 1997). (B) Highly speculative suggestion of the relationship between various segmental rhythm generators in the vertebrate embryo, the respiratory behaviours seen in lower vertebrates, and elements of the respiratory neuraxis in mammals.

Finally, I would suggest that while different segmental oscillators may have taken over primary roles associated with different respiratory behaviours, all oscillators are still entrained and still participate in each respiratory cycle. The production of any lung inflation event (from eupnea to gasping) with all of the nuances in timing and shaping of air flow requires the participation of all sites even though its phenotypic expression (inspiration) must be predominately mediated by the PreBötC.

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