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Neuroscience for Singers, Part 2: Anatomy, Physiology, and Motor Control of Breathing

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While the primary responsibility of the respiratory system is for sustaining/maintaining life, species have adapted this system to meet the demands of speaking and singing. The respiratory system is the power source for voicing. Control of the respiratory system incorporates a complex balance of inputs from the central nervous system (CNS) and peripheral nervous system (PNS), as well as the brainstem. A comprehensive understanding of the neuro-motor control of breathing is beyond the scope of this review, but we will provide an overview of the musculature of breathing, their innervations, and discussion of some of the areas of the motor cortex associated with voluntary breathing.

Fundamentally, ventilation (breathing) is dependent on pressure, volume, and contraction and relaxation of muscle. The respiratory pump can be conceptualized as three primary components: the thorax, the pulmonary system, and the abdomen. The thorax comprises the rib cage, thoracic muscles, and diaphragm. Within the thoracic cavity the pulmonary system (i.e., lungs), mediastinum, and the two pleural membranes are housed. The abdomen, then, is the portion of the trunk below the thorax, containing the viscera within a matrix of musculature, the relaxation and contraction of which play a considerable role in voluntary breathing.

Considering the pulmonary system, there are two lungs, the left and right. The right lung has three lobes (upper, middle, and lower), whereas the left lung has only two lobes (upper and lower). The airway is made up of the trachea, carina (where the trachea bifurcates), primary/main bronchi (leading to the right and left lungs), secondary/lobular bronchi (leading to the separate lobes), and tertiary bronchi (segmental portions of the lobes for each lung). The trachea, bronchial tree, and bronchioles have sympathetic and parasympathetic innervation. The sympathetic innervation arises from the T1-T4 (thoracic) spinal cord level, and causes bronchodilation (airways get bigger). The parasympathetic innervation comes from the medulla, and causes bronchoconstriction (airways get smaller). Within each bronchial we have cartilage (keeping the airway from collapsing) and smooth muscle (controlling diameter of airway). When we breathe in, oxygen (O_2) moves from the bronchioles into alveolar sacs where it is met with carbon dioxide

TABLE 1. Muscles of inspiration and expiration with innervations and actions.

Muscle	Role	Innervation	Action
*Diaphragm	Inspiration	Phrenic nerve (C3-C5)	Contracts to lengthen thoracic cavity and push abdominal wall out
External Intercostals	Inspiration	Intercostal nerve (T2-T6)	Elevates ribs
Sternocleidomastoid	Inspiration	Cranial nerve XI (accessory nerve)	Elevates upper ribs and sternum
Scalenes	Inspiration	Spinal nerves C2-C7	Elevates 1st rib
*Internal Intercostals	Expiration	Spinal nerves T1-T6	Reduces thoracic cavity. Pulls ribs down
External Oblique	Expiration	Intercostal nerves and subcostal nerve	Pulls lower ribs down and displaces abdominal contents inward
Internal Oblique	Expiration	Intercostal nerves and subcostal nerve	Pulls lower ribs down and abdomen in
Transversus abdominis	Expiration		Draws abdomen in
Rectus Abdominis	Expiration	Spinal nerve T5-L1	Pulls ribs and sternum downward
Latissimus dorsi	Expiration	Spinal nerve C6-C8	Reduces thoracic cavity

*Primary muscles of inspiration.

(CO_2) delivered via the pulmonary arteries. O_2 and CO_2 are exchanged in the pulmonary capillaries and oxygenated blood return to the heart via the pulmonary veins and CO_2 is removed through exhalation.

RESPIRATORY MUSCLES OF THE THORAX AND ABDOMEN

The cyclic movement of air in and out of the lungs is the primary role of the respiratory muscles.[1] Table 1 outlines the major muscles of inspiration and expiration, as well as their innervation from the CNS and spinal column. The muscles responsible for this harmonious action of breathing (delivering O_2, and removing CO_2) must work synergistically and without pause. The respiratory system is reliant on passive and active forces of these muscles. The ability of the system to exploit the passive forces of natural recoil of muscles, cartilages, and surrounding tissues, gravity, and surface tension of alveoli (air sacs in the lungs) reduces its energy expenditure. Wise singers maximize efficiency of the breath process by balancing the passive and active forces of breathing.

PRESSURE AND VOLUME

In order to understand the physiology of the lungs, we have to understand the relationship between pressures and volumes. Boyle's law states that pressure varies inversely with volume; as pressure increases, volume will decrease, and vice versa. Also recall that air flows from regions of higher pressure to lower pressure, seeking to equalize the two pressures. There are three types of pressures needed to understand pulmonary ventilation: atmospheric, intra-alveolar, and interpleural pressures. The atmospheric pressure is the pressure in the air surrounding the body. Intra-alveolar pressure is the pressure within the alveoli, which constantly changing throughout each phase of breathing. Finally, interpleural pressure is the pressure within the pleural cavities (visceral and parietal pleurae). Like intra-alveolar pressure, the interpleural pressure changes throughout the breach cycle.

With these pressures in mind, there are four main lung volumes we must define. First, tidal volume (TV) is the volume of air exchanged during a specific task. Inspiratory reserve volume (IRV) is the volume of air that can be inspired with a maximal effort. Expiratory reserve volume (ERV) is the volume of air that can be forced out with maximal effort. Residual volume (RV) is the volume of air that remains in the lungs after maximal expiration.

These four volumes are summed in different combinations to define various breath capacities for individuals. Understanding that each person has different capacities of lung volumes is helpful in understanding variations in

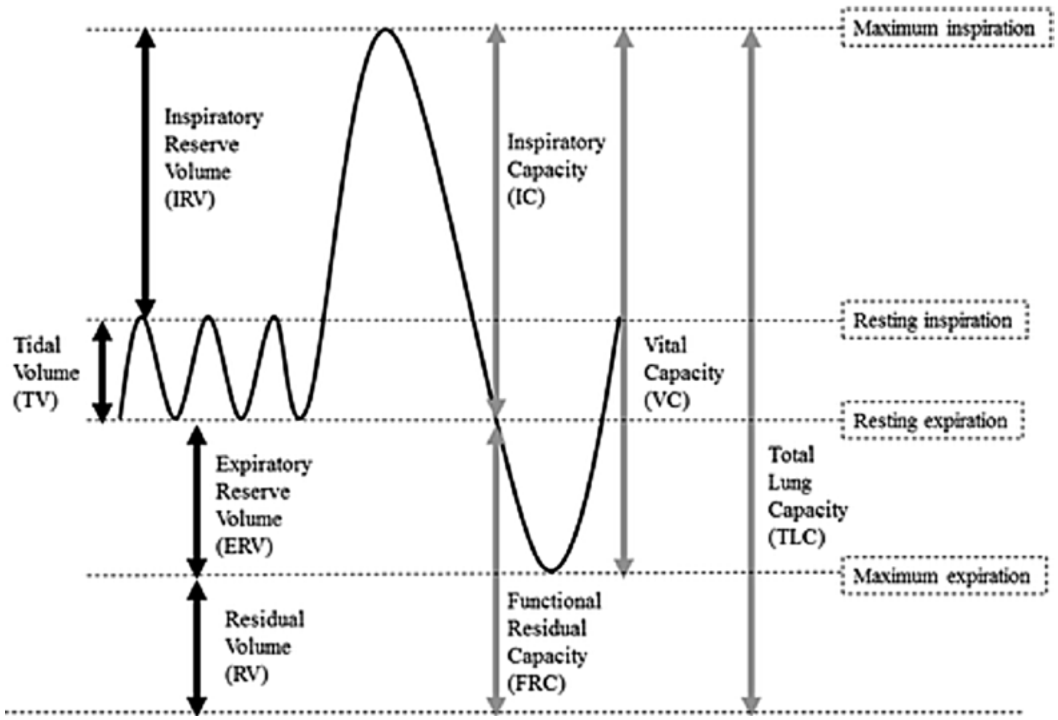

Figure 1. The physiological basis and clinical significance of lung volume measurements. From Mohamed Paisal Lutfi and Mohamed Faisal, *Multidisciplinary Respiratory Medicine* 12, no. 1 (December 2017): 3.

individual breathing function. The vital capacity (VC), or the volume of air that an individual can maximally inhaled following a maximal exhalation, is the sum of the IRV, TV, and ERV. Inspiratory capacity (IC) is the volume of air that can be inspired at the end expiratory point of tidal breathing and is calculated as the sum of IRV and TV. Functional residual capacity (FRC) is the volume of air contained in the lungs after the expiration phase of normal rest breathing, and is the sum of ERV and RV. Lastly, a person's total capacity (TC) is the total volume of air that can be contained in the lungs; it is the sum of IRV, ERV, and RV.

Returning to a view of the whole act of breathing, let us consider two different types of breathing: quiet or tidal breathing, and active breathing (sometimes called forced breathing). Quiet breathing is the breathing that is taking place at rest. The act of quiet breathing requires no cognitive effort and happens involuntarily. Active breathing is what is used for speaking, singing, exercise, etc.

THE PROCESS OF TIDAL BREATHING

Tidal breathing is maintained by the brainstem, more specifically the pons and medulla oblongata. The automatic process of tidal breathing relies heavily on incoming information from the central and peripheral nervous systems. Mechano- and chemoreceptors existing throughout the body send information to the brainstem regarding the arousal state of their surrounding tissues and their demands for oxygenation.[2] The brainstem then regulates tidal volume and rate in response to this information.

As we take a breath in, the airways are open and the respiratory pump is in its neutral position at the resting expiratory level (REL) (Figure 1). REL is the point at which the pressure within the lungs (alveolar pressure) equals the pressure outside the body (atmospheric pressure). In order to get air into the lungs, then, alveolar pressure must be decreased below atmospheric so air will flow in (recall that pressure and volume are inversely related). This reduction in alveolar pressure is produced through thoracic enlargement, which can take occur in several dimensions including vertically, anteroposteriorly, and transversely.

The diaphragm, the primary muscle for inspiration, is responsible for thoracic enlargement in the vertical dimension. The diaphragm is innervated by the phrenic nerve which receives both motor and sensory information, and is known to "keep the diaphragm alive." The diaphragm must contract during inspiration to lengthen the thoracic cavity and push the abdominal wall out. Simultaneously the external intercostals, sternocleidomastoids, and scalenes are elevating the ribs to accommodate this displacement. As the inspiratory muscles begin to relax, the thoracic cage decreases in size, at first passively due to elastic recoil of the cartilages and musculature and later actively via contractions of the internal intercostals. Correspondingly, interpleural and intra-alveolar pressure increases to be above atmospheric pressure. Initially, air begins to leave the alveoli with no additional muscle contraction.

RELAXATION PRESSURE CURVE

To better understand the passive and active contributors to exhalation, it is helpful to refer to a relaxation pressure curve (Figure 2).[3] The X-axis represents alveolar pressure measured in centimeters of water (cmH_2O); the Y-axis is percent vital capacity. A negative alveolar pressure indicates inspiration and a positive pressure indicates expiration. Relaxation pressure (black curve line) is produced entirely by nonmuscular forces. The amount of relaxation pressure is dependent upon how much the lungs are inflated (inspiration) or deflated (expiration) from the REL. At larger lung volumes (greater than REL) positive relaxation pressure is achieved. When the lung volumes are lower than REL, negative relaxation pressure results.

This process becomes increasingly more complicated as we begin to add on the contributions of muscle activation, because the relaxation pressure curve can be achieved at any lung volume through the use of muscular force. When alveolar pressure is more positive than the relaxation pressure curve (i.e., to the right of the curve), "net" *expiratory* pressure may be added to approximate the curve. Likewise, when alveolar pressure is more

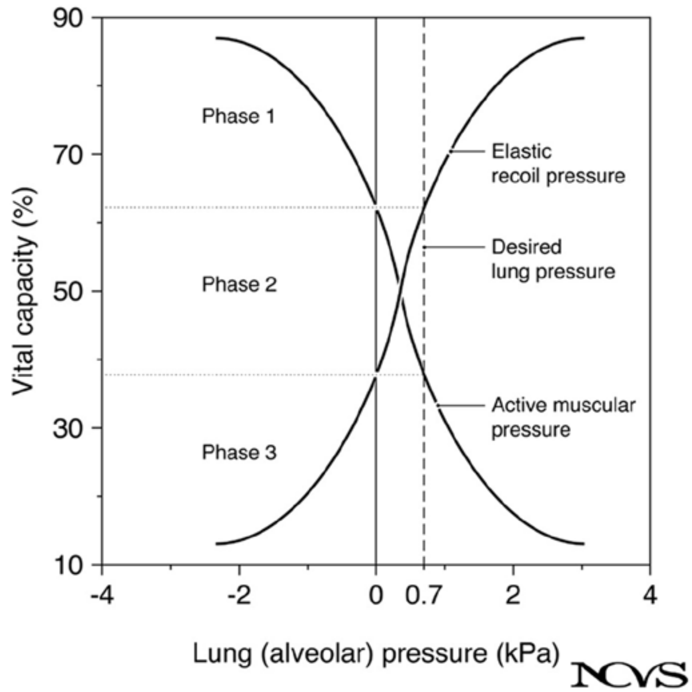

Figure 2. Relaxation/recoil pressure curve.

negative than that of the relaxation pressure curve, "net" *inspiratory* pressure may be added to approximate the curve. The opposite is true for the muscular pressure (still measured in cmH_2O). At larger lung volumes (inspiration) negative muscular pressure is needed to offset positive (expiratory) relaxation pressure.

For most speakers, speech is produced on the exhalation. On average, speakers initiate conversational speech at approximately 60% of VC (relaxation pressure curve). They continue speaking (exhaling) to about 38% VC. Speakers then refill the lungs to about 60% VC and the process is repeated. Speech initiation for a conversational loudness requires a pressure of about 10 cmH_20. During loud speech, the pressure requirements are greater, on the order of about 20 cmH2O. In order to meet these pressure requirements, speech is initiated at higher lung volumes. Some research findings suggest that this is also the case for singing, although more research is needed in this area.[4]

CORTICAL LOCI OF VOLUNTARY BREATHING

To this point, the neural regulation of breathing has been discussed in relation to involuntary breathing. While involuntary breathing is obviously necessary to sustain life, voluntary breathing is considerably more relevant to breathing for singing. The neural pathways governing voluntary breathing are largely similar to those of involuntary breathing with the primary exception of the locus of origin for their control. While involuntary breathing is initiated and sustained at the level of the brainstem, voluntary breathing is initiated and controlled in the motor cortex of the cerebrum. PET and fMRI imaging of the brain during voluntary breathing have determined areas in the superior motor cortex that appear to be associated with activation of the thoracic muscles of ventilation. Anterior to this region is a site associated with control of the diaphragm. Importantly, the same studies also observed bilateral activity in the sensory cortex, directly adjacent to the motor cortex regions, indicating afferent feedback from the lungs and thorax that was informing the motor control of the volitional breathing tasks being produced.[5]

NOTES

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The flowers that bloom in the spring, tra la,
Breathe promise of merry sunshine—
As we merrily dance and we sing, tra la,
We welcome the hope that they bring, tra la,
Of a summer of roses and wine.

Gilbert and Sullivan, *The Mikado*, II