PHYSIOLOGICAL REVIEWS
Vol. 69, No. 1, January 1989
Printed in USA.
Respiratory Functions of the Larynx
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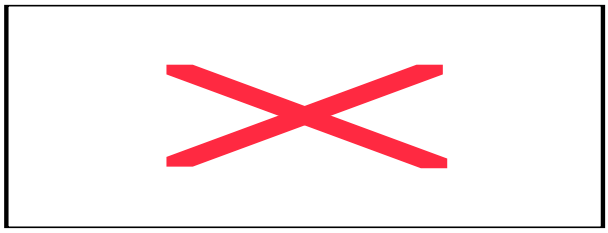

I. INTRODUCTION

The larynx is usually thought of as the organ of speech and song and as a protective valve that keeps unwanted materials out of the lower respiratory tract. Although vocal cord movements in concert with the breathing cycle have been recognized since ancient times (76), widespread interest in the role of the larynx in respiration has only developed fairly recently.

This review discusses the physiology of the larynx as a respiratory organ. This necessarily limited scope is expanded in some sections because other parts of the respiratory system interact with the larynx in many circumstances and because nonrespiratory aspects of laryngeal behavior are integrated with, and may compete with, respiratory mechanisms. At various times, the larynx participates in swallowing, coughing, laughing, vomiting, hiccuping, postural adjustments, and expulsive efforts, as well as in airway protection, vocalization, and breathing. Each of these functions is governed by a complex control system, but all involve the same lower motoneurons and laryngeal muscles. The behavior of the larynx in any circumstance depends on an integration of information from the various control systems. This integration takes place at several different levels in the central nervous system and constitutes an important aspect of laryngeal neurophysiology.

Laryngeal physiology has been reviewed and interpreted in a number of

articles and monographs (13,70,151,152,164,165,166,167,187,233). Other reviews, which deal with specific aspects of laryngeal function, are cited at suitable points in this review.

II. COMPARATIVE RESPIRATORY PHYSIOLOGY OF THE LARYNX

Although the mammalian larynx is the main focus of this review, brief consideration is given to the respiratory roles of the larynx in other vertebrate classes. This is a matter of considerable interest because the larynx is much more important as an organ of breathing in fish, amphibians, and reptiles than it is in most mammals and birds (13,14). Moreover, to the extent that the process of evolution can be deduced from the study of present-d speci es, the evidence strongly suggests that th e larynx played a crucial role in the development of successful air-breathing systems.

Several types of air-breathing mechanisms exist in teleost fish (66,108, 109,141,170,171,221). Among the most interesting species in this regard is the lungfish, animals with rudimentary larynges (151, 152, 231) capable of both aerial and aquatic respiration. In Protopterus, the most extensively studied variety, air breathing is accomplished by drawing air into the mouth and then forcing it through the larynx with positive pressure to inflate the lungs (141). Laryngeal closure holds the air in the lungs while the mouth is occupied with other activities, such as feeding or water breathing. When the animal 1s ready to take an other breath, the larynx relaxes,
escape fro m the lungs, and then the cycle is repeated.
allowing air to

A similar arrangement exists in the amphibians, although in this class the larynx is more highly developed and consists of a cartilage skeleton and paired dilator muscles in addition to muscles that close the glottic aperture (151,152,231). Like the lungfish, frogs and toads breathe by first drawing air into the oral cavity and then inflating the lungs by contraction of the muscles of the floor of the mouth. Expiration is achieved by opening the glottis and allowing the lungs to empty (51,111,229).

The oral force pump mechanism for filling the lungs with air serves lungfish and amphibians well. An inherent limitation, however, is that the tidal volume is constrained by the size of the oral cavity. Thus reptiles, some of which have high ventilatory requirements and small heads and mouths relative to their body size, draw air into their lungs by enlarging the chest cavity, much as birds and mammals do (171,221). In common with lungfish and amphibians, however, many reptiles breathe with an end-inspiratory breath-holding pattern in which air is held in the lungs for fairly long periods by closure of the laryngeal airway while the muscles of the ventilatory pump are relaxed (15, 24, 150, 179). This pattern of breathing is well suited to the needs of diving reptiles, such as turtles, and of snakes, which use the ventilatory muscles of the body wall for locomotion and other activities during laryngeal breath holding.

Although some diving mammals breathe with an end-inspiratory breath-holding pattern similar to that employed by reptiles (155,194), most mammals and birds use continuous tidal breathing, with the laryngeal airway remaining patent throughout the cycle. Thus the larynx is not essential for ventilation in homeotherms, although it influences breathing considerably, as described in sections III, IVC, and V.

In the evolution of vertebrate air-breathing mechanisms, the appearance of lungs in crossopterygian fish was an important early development (7, 178,223). These fish and the early amphibians presumably breathed by posi-

tive-pressure lung inflation and laryngeal breath holding, much as modern lungfish and amphibians do. Thus the larynx probably played an essential role in the evolutionary development of the vertebrate respiratory system, not only as a protective valve but also as an integral part of the breathing mechanism (13). With the emergence of aspiration breathing in reptiles and homeotherms, the importance of the larynx as an organ of ventilation diminished, although glottic breath holding is prominent in many modern reptiles and diving mammals and may play an important mechanical role in the breathing of some mammalian species during infancy (see sect. v).

The comparative anatomy and evolution of the larynx have been extensively reviewed by Negus (151, 152) and Wind (231). More recent articles by Tenney (221) and by Randall et al. (171) provide thoughtful analysis and interpretation of the comparative physiology and evolutionary history of vertebrate breathing mechanisms.

III. RESPIRATORY MOVEMENTS OF THE MAMMALIAN LARYNX

A. Functional Anatonay and Experimental Methods

The respiratory role of the extrathoracic or “upper” airways in mammals is the regulation of resistance to airflow rather than the production of airflow, as in many lower vertebrates (13). This role is complicated by the fact that subatmospheric pressure in the extrathoracic airways during inspiration tends to collapse them. Thus inspiratory narrowing or occlusion of the nasal or pharyngeal airway may occur in many circumstances (36, 38, 104, 105, 175), and upper airway resistance during inspiration tends to be unstable.

The larynx is anatomically protected from inspiratory collapse by its relatively rigid cartilage skeleton, particularly the cricoid cartilage, which forms a complete ring surrounding the laryngeal airway (165,232). Thus the laryngeal valve mechanism, consisting chiefly of the vocal cords and their attachments, can precisely regulate the transglottic pressure difference or resistance to flow in the course of both respiration and phonation (167). This fine tuning of upper airway, resistance is the laryngeal possible because, unlike other sections of the lumen is little influenced by moderate transmural pressure differences. The laryngeal valve acts more as an internal choke than as a Starling resistor. The anatomy of the larynx and the structures surrounding it is well described and illustrated by several authorities (70, 151, 165, 187, 232). Only features related to respiration are mentioned here.

Although laryngeal and tracheal airflow may be predominantly laminar in small animals (I&222), the resistance to flow through casts and models of the human larynx is flow dependent, owing to turbulence (52,156,191-193). The sharp reduction in airway cross-sectional area at the glottis gives rise to a central jet of high velocity in the upper trachea (143,156,203,226) during inspiration. This generates local turbulence even at Reynolds’ numbers below the value for fully developed turbulent flow (203).

The laryngeal jet is thought to influence both gas mixing and inertial deposition of particles downstream from the glottis during inspiration. Elongation of the velocity profile by the jet favors enhanced longitudinal gas mixing by Taylor dispersion (203, 226). On the other hand, dispersion is

reduced by fully developed turbulence, owing to flattening of the velocity profile (203). Studies with casts and models of hutman central airways suggest that the jet effect is largely offset by turbulence and that overall gas mixing is little affected by the larynx (143,203). However, the glottic jet may enhance inertial deposition of inhaled particles, especially at the carina (226).
Another situation in which the larynx may influence gas mixing is during purring in cats. This is a remarkable state in which glottic closure alternates with diaphragmatic contraction at a frequency of 20-30 Hz (157,176). During intense purring, the entire respiratory system vibrates, suggesting a parallel with the action of high-frequency ventilation devices, but the influence of purring on gas mixing has not been investigated.
The effectiveness of the larynx as a valve under conditions of complete closure is impressive. Intrathoracic pressures as high as 185 mmHg can be supported during voluntary Valsalva maneuvers (46), and transient values of 250-300 mmHg have been recorded during protracted coughing (196) and during weightlifting (46) in which breath holding helps to stabilize the thorax. Much of the ability of the closed glottis to withstand outwardly directed pressures seems to depend on the passive mechanical properties of the ventricular folds or false vocal cords (40,187). The false cords are said to be prominent in arboreal mammals, which presumably use Valsalva maneuvers for postural stabilization of the thorax while climbing (40). Inwardly directed pressures of up to 140 mmHg can be supported by the true vocal cords (40).
Complete closure is not the usual condition of the mammalian larynx, however, and primary consideration must be given to the behavior of the larynx in the course of normal breathing. Although varied and complex laryngeal movements occur during such activities as swallowing, coughing, and vocalization, most variations in laryngeal resistance during the normal breathing cycle take place at the level of the vocal cords. These bands of elastic tissue, covered by a delicate epithelium, are attached ventrally to the inner surface of the thyroid cartilage near the midline and extend dorsally to the vocal process of the arytenoid cartilage on each side. Vocal cord movements are accomplished by rotation of the arytenoids about their ligamentous attachments to the cricoid cartilage by the actions of intrinsic laryngeal muscles. Ventromedial rotation brings the vocal cords together in the midline, narrowing or closing the glottic airway. This action is brought about by contraction of the thyroarytenoid, interarytenoid, and lateral cricoarytenoid muscles (165,167,187). Ventrolateral rotation of the arytenoids abducts the vocal cords; this action is accomplished by a single pair of intrinsic muscles, the posterior cricoarytenoids (PCAs) (165, 167, 187). Each PCA muscle extends from a broad attachment on the posterior surface of the cricoid cartilage rostrally and laterally to its insertion on the muscular process of the arytenoid cartilage on the same side. Contraction of the PCA draws the muscular process in a dorsal and medial direction. This action pivots the arytenoid about the fulcrum of the cricoarytenoid ligament, thus drawing the vocal process laterally and widening the glottic airway.
The influence of the cricothyroid muscle on laryngeal airway caliber is complex. Contraction of this muscle tilts the thyroid cartilage ventrally and caudally with respect to the cricoid, thus lengthening and slightly adducting the vocal cords (5). When cricothyroid and PCA contractions occur simultaneously, however, the combined lengthening and abduction of the vocal cords make the glottic airway slightly larger than during PCA contraction alone (98,114).
The intrinsic laryngeal muscles mentioned are all innervated by vagal

motoneurons (67). The cricothyroid muscle is supplied by motor fibers in the external branch of the superior laryngeal nerve (SLN). All the other muscles are innervated by branches of the recurrent laryngeal nerve (RLN). The details of laryngeal muscle neuroanatomy are not presented here but are very thoroughly described by several authorities (77,206,233). The cell bodies of the motoneurons supplying the intrinsic muscles are located in the ipsilatera1 nucleus ambiguus; their precise locations have been mapped by retrograde axonal transport of horseradish peroxidase (49,160).

The respiratory movements of the cords may not be determined exclusively by the actions of intrinsic laryngeal muscles. Extrinsic muscles, extending from the thyroid and cricoid cartilages to the hyoid, the sternum, and other extralaryngeal structures, form a suspensory sling for the larynx (3,70, 144, 165). These muscles exhibit some phasic activity with the breathing cycle, especially in hyperpneic states (3,154, 180). The net effect of extrinsic muscle activity and of the intermittent caudal traction on the larynx by the trachea as a result of lung inflation is controversial and may vary with species and circumstances. Fink and colleagues (69-71) presented evidence that the whole larynx moves caudally during inspiration and rostrally during expiration. They suggest that these movements-are particularly prominent in humans, possibly owing to the caudal position of the human larynx. On the basis of these and other observations, they propose that an important mechanism of vocal cord abduction during inspiration is an unfolding and stretching of the larynx due to its inspiratory descent. On the other hand, Andrew (3), studying rats, and Mitchinson and Yoffey (144), studying human subjects, found no consistent pattern of rostrocaudal laryngeal movement with respiration. More recently Brancatisano and co-workers found no evidence of caudal displacement of the larynx during inspiration (31) and found a close association between vocal cord movements and electrical activity of the PCA muscles in awake human subjects (34). Thus the preponderance of evidence indicates that the respiratory movements of the cords are chiefly determined by intrinsic laryngeal muscle activity.

Laryngeal resistance to airflow is clearly regulated by vocal cord movements (6, 19, 43, 59, 106, 205), but the quantitative relationship between resistance and the size of the glottic aperture has not been well established. Experiments with cons tant airflo w through the larynx in cats show a roughly linear relationsh ,ip between conductance and glottic area or width at flow rates in the range of normal breathing (19,43).

Although laryngeal resistance is obviously variable and becomes infinite at times, several efforts have been made to estimate the contribution of the larynx to the total resistance of the respiratory airways under normal resting condi tion s. Measuremen ts of airflow and translaryngeal . pressure in human subjects breathing quietly through their mouths suggest that the resistance of the larynx is ~0.3 cmHzO l 1-l l s-l or -55% of total resistance (68,193).

The respiratory movements of the vocal cords have been investigated extensively in recent years. Several methods have been used to study these movements (13). In anesthetized animals and human subjects, inspiratory abduction and expiratory adduction of the cords can be seen by direct or indirect laryngoscopy (19,102, 172,195,205), and direct laryngeal photography can be used to record instantaneous glottic images (19). The amplitude and timing of vocal cord movements in anesthetized animals can be studied conveniently by directing air rostrally through the larynx at a constant flow rate while the animal breathes through a low, caudally directed tracheal

cannula. The resistance to this unidirectional flow through the larynx can be determined by recording the translaryngeal pressure difference (11, 12, 19, 42, 43, 54, 55, 209, 218-220). This method is influenced by artifacts, and the absolute resistance values determined by it may be seriously in error (44, 126). Nevertheless, the technique is a simple and reliable means of monitoring vocal cord movements, and it has been applied in very useful ways. A similar method has been used to measure respiratory changes in upper airway resistance in unanesthetized but restrained cats (157).

Laryngeal motor activity can also be assessed by electrophysiological methods. Bursts of activity in RLN occur with each breath (63, 83, 204). Functional interpretation of this activity is handicapped by the fact that it represents a mixture of impulses bound for abductor and adductor muscles

(13). Although inspiratory activity has often been considered to be abductor and expiratory activity to be adductor (63,83), these assumptions are unjustified; there is clear evidence, for example, that the PCA, an abductor muscle, is active during expiration in some conditions (19). This difficulty can be overcome by recording the activity in motor nerve branches serving specific laryngeal muscles (77) or by electromyography of individual muscles (8, 11, l&17,19,83,147,173). The latter technique has also been used in unanesthetized animals (159,174,176).

Respiratory movements of the human vocal cords can be seen with the aid of a laryngeal mirror (172, 195,205), but the movements are difficult to quantitate, and the unnatural oropharyngeal posture required limits the usefulness of this method for physiological studies. By contrast, fiber-optic laryngoscopy provides an excellent view of the glottis and permits tine or video records to be made over fairly long periods with little discomfort to the subject (6,58-60,97,106). Laryngeal electromyography in humans is generally an invasive, difficult technique (64, 85, 119). Recently, however, esophageal electrodes have been used to record PCA activity in both infants (117) and adult subjects (34,161). This is a very promising approach, which should lead to an improved understanding of PCA function in humans.

A cautionary note that applies to many of the techniques mentioned is that laryngeal motor activity is much more susceptible to depression by general anesthesia than are the movements of the respiratory bellows (26, 27). There is some evidence that the activity of vocal cord adductors is reduced more than the activity of other laryngeal muscles (197). The interpretation of results obtained from anesthetized animals must be tempered by these observations, as must those from animals and’human subjects treated with other sedatives (26,27,99).

The respiratory movements of the vocal cords have been examined in many circumstances, as reviewed elsewhere (13, 90). Because these movements constitute a large part of laryngeal respiratory physiology, they are considered in some detail.

B. Quiet Breathing

In resting or anesthetized animals the cords are abducted during inspiration, providing a widely patent laryngeal airway. During expiration, they are less widely separated and may approach each other rather closely in the midline (11, 19, 43, 151, 209). Similar cord movements have been found in species as diverse as rats (142) and horses (82). The magnitude and time course of these movements vary among individual animals, species, and circumstances, but the general pattern is consistent. Measurements of laryngeal resistance confirm that the glottis is more widely open during inspiration than during expiration (11, 19, 139, 140,219,220).

Electromyography indicates that the inspiratory opening of the laryngeal airways is chiefly the result of phasic activation of the PCA muscles (11, 40
12,19,147,212), although synergistic contraction of the cricothyroid muscles may also contribute, as described in the previous section (74,114,213). Which muscles are responsible for the expiratory narrowing of the glottis is much less certain. Rats exhibit consistent vocal cord adductor activity in expiration (197), and a similar pattern is common in infant animals of several species (90). On the other hand, others have found little adductor activity in quiet breathing (11,19,147). In some studies, the cords have been found to be more widely separated in all phases of the breathing cycle than they are after muscle paralysis or death (11, 19, 195), suggesting a net abductor influence even during expiration. Thus the most consistent mechanism underlying cord movements in resting animals is PCA contraction during inspiration and PCA relaxation, permitting passive recoil, during expiration. The cricothyroids and adductor muscles, such as the thyroarytenoids, may play supporting roles in some circumstances.

Vocal cord movements in resting human subjects have been examined extensively by fiber-optic laryngoscopy (31,34,58-60,97), and the pattern is very similar to that described in other mammals. During quiet breathing, there is little or no rostrocaudal movement of the larynx, suggesting that cord movements result chiefly from intrinsic laryngeal muscle activity rather than from the unfolding mechanism proposed by Fink (70). Moreover, records of PCA activity recorded by a retrolaryngeal electrode placed high in the esophagus show a strong pattern of inspiratory PCA activation (34).

The respiratory movements of the vocal cords are closely coordinated with those of the diaphragm and other muscles of the ventilatory pump. The cords begin to separate slightly before the onset of diaphragmatic contraction (59, El), and this pattern reflects earlier activation of laryngeal motoneurons rather than differences in the time required for nerve conduction or the initiation of muscle contraction (45,204,197). This schedule of activation is mechanically advantageous, since it opens the laryngeal airway just before the onset of airflow, thus avoiding the inefficiency of diaphragmatic contraction against a partially or completely closed glottis. This pattern is seen in all normal states and even persists in apneusis (204). The time by which the onset of RLN discharge leads that of the phrenic nerve is much reduced after vagotomy, and the order of onset is reversed during gasping in medullary animals (204).

C. Reflex Modification of Breathing Movements

Like other ventilatory movements, those of the vocal cords are influenced by reflexes arising from receptors in the respiratory tract and body wall. Afferents from the laryngeal mucosa (see sect. IVC) inhibit inspiratory movements and either exaggerate the expiratory adduction of the cords or induce sustained glottic closure (107, 219). Irritant stimulation of the nasal airway elicits similar responses via afferents in the trigeminal nerves (219).

Stimulation of pulmonary irritant receptors and C-fibers also enhances expiratory laryngeal closure (209). Expiratory narrowing is increased during bronchoconstriction induced by provocative maneuvers in asthmatic patients (97). In anesthetized animals, ammonia vapor or dust inhalation, experimental anaphylaxis, pneumothorax with lung collapse, and a variety of bronchoconstrictive drugs all cause laryngeal narrowing in expiration (54, 81, 209, 217, ZZO), probably by lung irritant receptor stimulation. Phenyl diguanide

injections (209) and experimental pulmonary edema (81) have similar reflex effects, perhaps as a result of C-fiber stimulation.

Lung volume, and thus activity of pulmonary stretch receptors, has complex effects on laryngeal behavior that do not simply correspond to the influence of lung volume on the breathing pattern (8,, 19, 54, 63, 75,83,140). For example, inflation of the lungs during expiration in anesthetized cats has been reported to induce tonic activation of the PCA muscles but to delay the onset of the next inspiratory burst of PCA activity (19). In this situation the PCA exhibits functional characteristics of both inspiratory and expiratory muscles, an appropriate pattern of response, since the vocal cords guard the portal of airflow in both inspiratory and expiratory directions.

The most important responses to lung inflation, however, are those that occur when the animal inflates its own lungs during inspiration rather than those that are induced by experimental inflations at unnatural times in the breathing cycle. Many investigators, beginning with Breuer (35), have examined the influence of inspiratory lung inflation by preventing inflation during occasional breaths, usually by occluding the airway. Studies of laryngeal responses to this kind of maneuver reveal vigorous inspiratory PCA or RLN responses to noninflation, which reflect inflation-induced inhibition of vocal cord abduction during unhindered breaths (45,120,202,227).

Laryngeal movements are also influenced by afferents in intercostal nerves. The laryngeal responses to experimental stimulation of these nerves are complex, varying with the anatomic level of the nerve that is stimulated and with the timing of the stimulation in the ventilatory cycle. Midinspiratory electrical stimulation of external intercostal nerves at the midthoracic level (T5 or T6) inhibits RLN and PCA activity in anesthetized cats (173), whereas stimulation at a more caudal level (T9 or TlO) may cause brief excitation before inhibition (173, 197). Intercostal nerve stimulation during expiration activates both the PCA and the thyroarytenoid muscle, a vocal cord adductor (173, 197). These responses are difficult to interpret in purely respiratory terms, and they may reflect the activity of postural control systems.

D. Hypoxemic States

to

Laryngeal breathing movements participate in the ventilatory responses chemical stimulation in both human and animal subjects. In hypercapnia, the most frequently studied condition of this kind, the vocal cords are more widely abducted during inspiration than in the resting state, and the abduction is prolonged into or through the expiratory period, thus sharply reducing expiratory laryngeal resistance (11,19,42,139,147). This pattern of response accommodates the increased expiratory flow rates that occur in hypercapnia and is also seen in human subjects during muscular exercise (58) and in cats during hyperthermia (55).

Because increases in ventilation alter the pattern and intensity of pulmonary receptor discharge, vagal afferents must play some part in determining the behavior of the larynx in hyperpneic states. As mentioned, lung inflation inhibits laryngeal abduction during inspiration. Thus the wide inspiratory abduction that occurs in hypercapnia and exercise must reflect an increased central command to the PCA muscles that overcomes the inflation-induced inhibition.

The laryngeal response to hypoxia in most vagally intact animals is similar to that found in hypercapnia (11, 12), but much evidence indicates that the hypoxic situation is neurologically more complex. After vagotomy caudal to the RLNs, hypoxia elicits expiratory adduction of the cords, and

tests with cyanide indicate that this effect is the result of carotid body chemostimulation (l&54). This. adductor influence of peripheral chemoreceptor stimulation is counteracted in vagally intact animals by pulmonary afferents, probably from stretch receptors (l&17).

Isocapnic hypoxia in human subjects elicits responses that resemble those in vagotomized cats, i.e., the cords are .more adducted in expiration than they are at the same level of ventilation in hypercapnia (60). This pattern presumably reflects the expiratory vocal cord adducting influence of peripheral chemoreceptor stimulation that is revealed by vagotomy in animals (12, 54). Its appearance in vagally intact humans may reflect the relatively weak reflex responses to pulmonary stretch receptor afferents in conscious humans noted by Guz et al. (84).

Hypocapnia is a potent vocal cord adductor influence during expiration (9,11,23,147), and this factor must be considered in studies with hypoxia in which CO_2 is uncontrolled.

In summary, the responses of the larynx in hyperpneic states, especially during expiration, depend on the relative strengths of several influences. Afferents from central chemoreceptors and from pulmonary stretch receptors and an influence related to ventilatory drive favor expiratory abduction of the cords, with a resultant decrease in the resistance of the larynx to expiratory flow. These influences are opposed by peripheral chemoreceptor afferents and by hypocapnia, factors that favor vocal cord adduction during expiration.

E. Sleep

Recently many studies of respiration in sleep have appeared, and several investigators have made careful observations of laryngeal behavior in sleep. Orem and colle agues (157-X9), in a series of studies on . unmed .icated but restra ined and tracheostomized ca ts, found that upper airway resistance increased in sleep, particularly in rapid eye movement sleep (REMS). This increase in resistance was accompanied by decreased PCA electromyographic activity, especially in expiration. Megirian and Sherrey (142), studying rats, found little change in laryngeal muscle activity with the onset of slow-wave sleep (SWS), but some reduction in activity was found during REMS. .An interesting feature of their work is that rats in SWS, when made hypoxic, developed expiratory glottic narrowing as a result of reduction in expiratory PCA activity and recruitment of adductor discharge. This response to hypoxia is similar to that seen in anesthetized, vagotomized cats (19) and in awake humans (60), as described in the preceding section.

Studies of laryngeal muscle activity in dogs showed little change in PCA discharge during SWS and in some cases showed an increase during REMS (61,92). Thus the behavior of the larynx during sleep appears to vary among species and experimental preparations.

F. Voluntary Breathing Eflbrts

In human subjects, voluntary hyperventilation attenuates the expiratory narrowing of the glottic airway, and the pattern of vocal cord movements closely resembles that seen in exercise and hypercapnia (16). Despite the hypocapnic closure of the larynx that occurs in animals (9,11,23,147), the laryngeal movements accompanying voluntary hyperventilation were essentially the same whether or not hypocapnia was allowed to develop (16). Thus, in this case, the abductor activation that accompanied the voluntary hyperventilation overrode whatever hypocapnic adductor influence may have been present.

The behavior of the larynx during voluntary panting has been studied to assess the laryngeal contribution to the values of airway resistance measured

by whole body plethysmography. The vocal cords are widely abducted with little movement during unrestricted panting (6, 106, 205), although panting with voluntary restriction of flow or volume may be associated with some narrowing of the glottic airway (205).

Forced expiration, as performed in pulmonary function testing, is accompanied by abduction of the vocal cords (33). Because this abduction is not seen during the passive expulsion of air by sudden chest compression during relaxed expiration, the most likely explanation is that the abductor muscles are coactivated along with those of the respiratory pump as a part of the expiratory effort (33).

G. Mechanical Loads

Several investigators examined the responses of the larynx to experimental changes in the resistance of the respiratory system. These changes consisted of loading the system by adding external resistances and of unloading it by opening the mouth or by a tracheostomy.

Resistive loading and airway occlusion during inspiration have been found to increase the inspiratory activity of laryngeal abductors in decerebrate or anesthetized animals (45, 54, 120, 188, 202, 22'7), due chiefly to the action of the Hering-Breuer reflex, discussed in section IIIC. Changes in chemical drive may also have played a role in some of the experiments. Dixon et al. (54) found that airway occlusion induced closure of the glottis, possibly owing to a protective reflex elicited by airway distortion during the attempted inspiration. The unloading of the respiratory system by means of a tracheostomy was found by Sasaki et al. (188) to decrease phasic inspiratory RCA activity.

The application and removal of loads during expiration yielded varied results. Rattenborg (172), studying human subjects, and Remmers and Bartlett (174), working with unanesthetized cats, found compensatory responses in laryngeal behavior, suggesting active regulation of tracheal pressure or of the time course of lung deflation during expiration. More recent studies, however, in which the human vocal cords were monitored by fiber-optic laryngoscopy, showed expiratory narrowing of the glottic airway in response to expiratory resistive loads (32, 47). Thus, at least in some circumstances, the addition of an external resistive load during expiration elicits an increase in the internal laryngeal resistance as well.

H. Miscellanmus Conditions

Although the larynx is involved in a large number of activities, a few merit special attention. One of these is feline purring (176), in which a reciprocal oscillation of activities of vocal cord adductors and abductors causes glottic closure and reopening every 35-50 ms throughout the respiratory cycle. During inspiration, this oscillation is coordinated with a gated activity of the diaphragm at the same frequency so that the diaphragm is active only when the glottis is open. The neurological basis of purring is not fully worked out, but the timing of the diaphragmatic and laryngeal components appears to depend on the activity of a central nervous system oscillator rather than on reflex feedback (176). The fact that inspiratory flow can be interrupted 20-30 times in each breath without seriously disturbing ventilatory function attests to the intricate integration between the neural control systems that serve purring and breathing.

Other conditions that interact with the ventilatory role of the larynx include hiccups and sighs or augmented breaths. In hiccups, the diaphragm contracts spasmodically but excessive inspiratory airflow is prevented by rapid closure of the glottis (153). It is noteworthy that in patients in whom the larynx is bypassed by a tracheostomy (153) or by an endotracheal tube

(39), hiccups result in severe respiratory alkalosis.

Augmented breaths, in which renewed inspiratory effort is superimposed near the end of an ordinary inspiration (10, 80), are accompanied by appropriate laryngeal movements, which accommodate the increased airflow (218).

Although patients and animals with tracheostomies are able to cough (124, 125), the effectiveness of coughing in clearing secretions from the airways is considerably greater when the larynx is in the breathing circuit. Both reflex and voluntary coughs are initiated by an inspiration of variable depth (124,125,130,228). When this preparatory inspiration exceeds the base-line tidal volume, the increased inspiratory effort is accompanied by exaggerated abduction of the vocal cords. The next phase, absent if the subject has a tracheostomy, is one of compression. The glottis is tightly closed, and expiratory muscles contract, typically raising intrapulmonary pressure quickly to levels that decrease lung volume appreciably by compression (125,228). The duration of the compression phase is -200 ms in humans. It is terminated abruptly by an explosive abduction of the cords, which releases the compressed gas both by expansion and under continued force exerted by the expiratory muscles. The coughing maneuver results in extensive dynamic compression of intrathoracic airways, which, coupled with the high rate of airflow, results in very high linear velocities of air movement through the narrowed segments. These high airstream velocities account for the effectiveness of cough in clearing debris from the airways. The mechanism of coughing has been the subject of recent reviews (124,125,130).

Vocalization, including speech, singing, whispering, and the production of other sounds, is an activity in which the larynx is heavily involved and in which breathing is greatly modified. This topic is beyond the scope of this review but has been examined and reported extensively by several authorities (88, 167, 168).

I. Physiological Significixnce of Laryngeal Breathing Movements

The significance of the respiratory movements of the vocal cords is best considered in the context of the mechanical properties of the whole respiratory system (13,234). Because inspiration and expiration are fundamentally different in mechanical terms, these two phases must be considered separately.

In inspiration, the energy for airflow is provided by the muscles of the ventilatory pump, and the rate of airflow is determined by the force generated by these muscles and by the resistance and elastance of the system. Vocal cord movements influence this process to the extent that they influence airway resistance (19, 59). The duration of inspiratory flow is’chiefly determined by the duration of neural activation of the muscles of the ventilatory pump, although mechanical factors may produce some discrepancies between the durations of neural and mechanical inspiration (177,235,236).

In contrast, the energy for expiratory airflow under resting conditions is derived from the potential energy stored in the system by displacement from its relaxed position during the previous inspiration. Thus the rate and duration of passive expiratory flow depend on the recoil pressure and the mechanical properties of the system rather than on muscle activity. There is no logical requirement that the duration of expiratory airflow be as long as neural expiratory duration, and in fact the time required for passive collapse of the relaxed, intubated respiratory system is much shorter than the observed duration of expiration during quiet breathing (37, 78). Most animals do not have an appreciable end-expiratory pause in airflow, and it appears that this matching of expiratory flow to expiratory time is achieved by the

slowing of airflow by postinspiratory pliometric contraction of inspiratory muscles (37, 78, 79, 148, 162) and by partial closure of the laryngeal airway (19, 59). These expiratory braking mechanisms appear to be under vagally mediated control, at least in the cat (174) and possibly in human subjects as well (172). Because the mechanical history of expiration influences the time of onset of the next inspiration by volume-related feedback (20, 35, 47, 113, 174), the larynx appears to play a significant role in determining the respiratory frequency (13).

IV. LARYNGEAL AFFERENTS AND THEIR REFLEX ACTIONS

In keeping with its many physiological roles and the need for several types of feedback control, the larynx has a rich sensory innervation. A few afferent fibers run in the RLNs (181,211), but by far the major share are in the SLNs, chiefly in the internal branches (137, 230, 233). As noted by Sant'Ambrogio et al. (183), the internal branch of the SLN of the cat contains ~2,200 myelinated afferent fibers (57) compared with ~3,000 in the cervical vagus, which supplies most of the thoracic and abdominal viscera (1). These numbers emphasize the abundance of sensory information that the larynx provides relative to its size.

Many investigators have recorded the activity of single afferent fibers in the SLN (4,25,29,48,50,72,112,132,136,181-185,199-201,210). The literature is confusing because different classification schemes have been adopted by different workers. Detailed reviews of laryngeal receptor physiology have been published by Wyke and Kirchner (233) and Widdicombe (230).

A. Mechanoreceptors

The most thoroughly investigated general category of laryngeal receptors are those responding to displacement or deformation, i.e., mechanoreceptors. Sampson and Eyzaguirre (181) distinguished "touch" receptors, lying in or near the laryngeal mucosa, and "deep" mechanoreceptors, which appeared to be located in the laryngeal muscles or joints. Boushey et al. (29) classified mechanoreceptors in two groups, depending on their spontaneous activity: group 1 fibers had little or no spontaneous.activity and most adapted quickly after mechanical stimulation, whereas group 2 fibers were spontaneously active and showed slow and incomplete adaptation. Group 1 units were stimulated by ammonia, S02, and COZ, whereas those in group z were unaffected by SO2 and inhibited by C02. Recent studies by Davis and Nail (48,50), using similar classification criteria ("silent" and "tonic" receptors), confirm many of the findings of Boushey et al. (29) and provide a detailed description of the responses of both types of receptors to static and dynamic (vibratory) mechanical stimulation.

Hwang et al. (101) studied the responses of SLN afferents to sustained changes in transmural pressure of the isolated upper airway in cats. Although some of the units studied were initially silent, all responded to positive or negative pressure steps and most adapted slowly and incompletely to sustained transmural pressure differences.

In a series of investigations, Sant'Ambrogio and colleagues (136, 182-185) used a spontaneously breathing animal preparation, employing a T-tube tracheotomy, to identify and classify laryngeal receptors, according to their responses to transmural pressure, airflow, and laryngeal movements. By use of this preparation, which enables the investigator to direct the respiratory airflow through the upper airway or to divert it through the tracheotomy, three types of receptors were identified and characterized. "Pressure" receptors, many of them tonically active, show slowly adapting increases in activity in response to collapsing or less commonly distending transmural pressures in the larynx (136,183). These receptors are similar to the "group

2" receptors of Boushey and co-workers (29) and the "tonic" units of Davis and Nail (48, 50). "Flow" receptors, initially identified by their response to airflow through the larynx (183), have subsequently been found to be **"cold"** receptors, which are activated by convective and evaporative cooling of the laryngeal mucosa during inspiration (182, 185). These units, which are insensitive to gentle mechanical stimulation, do not correspond to the "silent" receptors of Davis, which responded to local probing and were not consistently activated by cold air or saline (48). Finally, some receptors ("drive" receptors) are activated by laryngeal movements accompanying the breathing cycle (183, 184). Some of these units become inactive during laryngeal muscle paralysis by cold blockade of the RLNs, but others are activated entirely or in part by transmitted tracheal motion (184).

B. Chemoreceptors

In addition to the responses of some mechanoreceptors to chemical,stimuli, the larynx contains receptors with activity that is determined by the chemical composition of fluids placed in the laryngeal lumen. The responses of these receptors to a variety of liquids have been investigated by several workers (25, 29, 93, 128, 199-201, 208). The most striking response of these units is to intralaryngeal water; this leads to sustained afferent fiber discharge until the water is flushed from the larynx with normal saline or some other nonstimulating fluid. The chemical basis of the water response may vary among species. In dogs and rabbits, the chief stimulus is the reduction in chloride ion concentration (25, 29, 199, 200). However, chloride has little influence on the laryngeal water receptors of rats (201), and those of lambs respond to a variety of salts and sugars (93). The structural nature of the laryngeal chemoreceptors has not been established; some evidence suggests 'that they may be free, unmyelinated nerve endings (25,93).

In addition to the "water" receptors, which have been studied rather extensively, the larynx contains other nerve endings with known or suspected chemoreceptor functions. A few supraglottic taste receptors, responding to numerous substances, have afferents in the SLN (207). In addition, laryngeal paraganglia, with histological features that closely resemble those of the carotid body, have been found in several species, including humans (123). The possibility that these paraganglia have a chemoreceptor role seems likely, but no studies of their function appear to have been done.

C. Responses to Laryngeal Stimulation

The larynx is a rich source of consciously perceived sensations. Although few formal studies of laryngeal sensations have been done (for discussion see Ref. 230), the feelings of laryngeal discomfort that result from inhaled irritants or misplaced food particles are common experiences. Similar sensations are elicited if the tip of an exploring fiber-optic laryngoscope touches the unanesthetized vocal cords. In view of the superficial nature of the effective stimuli and the limited duration of most laryngeal sensations, it seems likely that the responsible receptors are located in the mucosa and are rapidly adapting. It is much less clear what receptors or stimuli are involved in the laryngeal aching or feeling of fullness (globus sensation) reported by some people during emotional stress.

The most prominent reflex response to laryngeal mucosal stimulation is the immediate tight closure of the glottis (17,219). This protective response fulfills one of the most fundamental roles for which the larynx has evolved, that of protecting the lower respiratory tract from contamination with harmful materials. However, even this most primitive laryngeal response must be considered in the context of the larynx's other fundamental role, that of breathing. Closure of the glottis requires that airflow cease, and it is

not surprising that the reflex control of protective laryngeal closure is closely integrated with the control of the breathing cycle.

Weak mechanical or chemical stimulation of the laryngeal mucosa exaggerates the expiratory adduction of the vocal cords but does not interrupt breathing (214-216, 219). More intense stimulation elicits apnea and tonic laryngeal closure, sometimes interrupted by coughing (107,219). Associated responses include bradycardia (224), bronchoconstriction (28, 149, 224), and an increase in the rate of mucus secretion in the respiratory tract (163).

Beyond these protective reflexes, laryngeal afferents also mediate changes in the intensity and pattern of breathing movements. Although first identified more than 50 years ago (86), the laryngeal reflex modification of ventilatory efforts has received renewed attention recently because of possible involvement in the pathogenesis of obstructive apnea during sleep. Subatmospheric pressure in the upper airway has been found to enhance the inspiratory activities of several upper airway dilating muscles (133-135227) or their motor nerves (100). The response is greatly reduced after section of the SLNs. This reflex system is well designed to prevent or relieve upper airway obstruction at the oropharyngeal level; airway closure in this region increases the amplitude of inspiratory negative pressure swings in the larynx, thus stimulating laryngeal receptors and increasing the inspiratory activity of dilator muscles. The receptors responsible for this reflex have not been identified but are likely to be the slowly adapting “pressure” receptors (136, 183) in view of the nature of the stimulus and the sustained nature of the reflex response.

An extensive literature reports results of electrical stimulation of the SLN (21,22,87,103,121,122,127,131,190,214-216). The functional interpretation of these studies is clouded by uncertainty about the types of afferents that are activated and the characteristics of their natural stimuli. Nevertheless, this technique has proved to be a useful tool for investigating the quantitative influence of other factors on laryngeal reflex responses (87,103,122, 190) and for exploring some features of the central respiratory control mechanism (21,22,121).

For a more detailed treatment of laryngeal afferents and their reflex effects, there are reviews by Korpas and Tomori (115) and by Widdicombe (230).

V. THE INFANT LARYNX

The purpose of this article is to review the entire scope of laryngeal respiratory physiology rather than to focus on any single topic or circumstance. Nevertheless, several of the mechanisms discussed are of special interest or importance during development and merit consideration in this context. Reviews of the subject have been published by Harding (90) and Trippenbach (225).

The larynx participates in fetal breathing movements (53, 89, 94) and may play a part in controlling the flow of fetal lung fluid out into the amniotic sac (91, 95).

After birth the larynx serves as a valve regulating airflow, and there are important differences in this regard between neonates and adults of the same species. Whereas in adults the vocal cord adductor muscles show little activity during quiet breathing (19, 94), in neonates the adductors seem to be active during most expirations (94), sometimes occluding the airway so that expiratory flow is interrupted. This pattern is particularly prominent in newborn opossums, which perform end-inspiratory breath holds supported by the larynx during the first few weeks of life in their mother’s pouch (65). With maturation, the young opossums convert to a conventional continuous

breathing pattern but usually revert to end-inspiratory breath holding if they are made hypoxic (65). In lambs, expiratory adductor activity is apparent soon after birth, and it increases in prominence during the first few weeks of life and then diminishes (94). A somewhat different developmental pattern is seen in dogs (62, 186, 189). Human infants interrupt expiratory airflow quite often during the first few hours of extrauterine life (73, 169), and it must be suspected that this interruption occurs at the level of the larynx.

The prominent vocal cord adductor activity in neonates provides them with a mechanism for retarding expiratory flow, thus preserving lung volume, a useful device in the presence of stiff lungs housed in a compliant chest wall (73,89,146). Both laryngeal activity (89) and the duration of expiration (116) are influenced by the volume history of the system during expiration. Rapid collapse enhances the activity of laryngeal adductors and shortens the expiratory period, both of which seem to keep end-expiratory volume advantageously above the relaxed functional residual capacity (118, 145). As pointed out by Bryan and England (41), however, some doubt must be cast on this interpretation, since during REM sleep, the predominant state of neonates, the laryngeal adductors show little activity (6289) and end-expiratory volume falls (96).

Reflexes from the larynx also exhibit special features in newborn animals. Whereas mild inhibition of breathing may occur in adult animals when air flow is directed through the upper airway (86,129,138), this response is much more pronounced in neonates of several species (2). Moreover, when water and some other liquids are placed in the larynx, newborn animals respond with a sustained apnea (25, 56, 110, 128), which may even lead to death> unless the offending material is removed by flushing the region with saline. This response is mediated by afferents in the SLN. Laryngeal closure is not always a part of the response (25), although this finding is complicated by the influence of general anesthesia on adductor activity (198). The apneic response diminishes with age and is replaced by coughing as the chief response to intralaryngeal water in adult animals. This change apparently reflects maturation of the central nervous system rather than the laryngeal receptors, since receptor responses are similar in neonates and adults (25). The importance of this apneic response in protecting the lungs of baby animals from aspiration injury is apparent, but the inhibition of breathing is so profound that some investigators have speculated that it may be a cause of sudden infant death. In this regard it may be important that hypoxia favors vocal cord adduction, as shown most clearly in young opossums (65), and that sustained hypoxia depresses breathing in infants (30). Thus reflex apnea and laryngeal closure, induced initially by milk or gastric contents in the larynx, might be sustained and intensified by the resultant progressive hypoxia. Hypercapnia might counteract this process in view of its laryngeal dilator action (19,54). In any case the eventual outcome of a prolonged apneic spell must depend on the balance of many factors, including the depressant action of severe asphyxia.

VI. CONCLUDING REMARKS

The larynx has long been recognized as a multipurpose organ. With regard to respiration, its primary role has usually been seen as a protective one, that of guarding the airway entrance against ingested, regurgitated, or inhaled materials that might injure the lower respiratory tract.

Recently, interest has been directed at other roles of the larynx in the physiology of breathing. Studies in lower vertebrates and in both adult and neonatal mammals have established the importance of the larynx as a valve

that influences airflow, particularly during expiration. Furthermore, laryngeal receptors and the reflexes arising from them have been subjected to renewed investigation. Here, too, some of the most important findings are in neonates, and these raise the question of a possible laryngeal role in the sudden infant death syndrome.

The larynx is daunting in its complexity with regard to fluid mechanics, muscle action, and neural control mechanisms. It participates in a large number of functions, all of which must be coordinated with respiration. The success with which the larynx manages its duties is a tribute to the time-sharing principle, which it employs extensively. Long excluded from most respiratory experiments by tracheal cannulas or endotracheal tubes, it is gaining recognition as an important part of the respiratory system.

I thank Edith Coates, Terry Hall, Susan Knuth, and Dale Ward for their help in the preparation of this review.

Financial support was provided by National Heart, Lung, and Blood Institute Grant
HL-19827.

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