REVIEW ARTICLE

Coordination of mastication, swallowing and breathing

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Summary The pathways for air and food cross in the pharynx. In breathing, air may flow through either the nose or the mouth; it always flows through the pharynx. During swallowing, the pharynx changes from an airway to a food channel. The pharynx is isolated from the nasal cavity and lower airway by velopharyngeal and laryngeal closure during the pharyngeal swallow. During mastication, the food bolus accumulates in the pharynx prior to swallow initiation. The structures in the oral cavity, pharynx and larynx serve multiple functions in breathing, speaking, mastication and swallowing. Thus, the fine temporal coordination of feeding among breathing, mastication and swallowing is essential to provide proper food nutrition and to prevent pulmonary aspiration. This review paper will review the temporo-spatial coordination of the movements of oral, pharyngeal, and laryngeal structures during mastication and swallowing, and temporal coordination between breathing, mastication, and swallowing.

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1. Introduction

The pathways for food and air cross in the pharynx. In breathing, air may flow through either the nose or the mouth; it always flows through the pharynx. When we swallow, the pharynx becomes a passage for food. This passage is separated from the lower airway and nasal cavity during the pharyngeal swallow to prevent aspiration of foreign materials into the trachea before or during swallowing. When eating solid food, mastication occurs in the oral cavity respiration continues through the nasal cavity and pharynx. The two functions, mastication and breathing, appear to occur in different areas. In reality, however, food is collected in the pharynx during eating [1,2]. Chewed food is gradually transported through the faucae and is collected in the oropharynx or valleculae, where the bolus is formed prior to swallowing. Bolus transport and positioning prior to swallow initiation vary depending on physical characteristics of the food [3,4]. While the bolus is collecting in the pharynx, breathing continues in the same anatomical space. When the swallow is initiated, the collection of food in the pharynx is combined with the transported food bolus from the mouth, and propelled through the pharynx to the esophagus. Because feeding and breathing share the same anatomical space, the fine temporal coordination of feeding and breathing is essential to provide proper nutrition and to prevent pulmonary aspiration and its sequelae. The aim of this review is to describe current understandings of the tempo-spatial coordination of the movements of the structures of the oral cavity, larynx, and pharynx during mastication and swallowing, and define the coordination of breathing and eating. This review does not address the neural control or coordination of eating and breathing or animal models of feeding. Several other review articles are available [5,6].

2. Anatomy

Feeding and breathing share the same anatomy. The pharynx is a route for breathing and feeding (mastication and swallowing) but is used in different ways. The pharyngeal cavity consists of the muscles of the soft palate, tongue, epiglottis, and pharyngeal walls, and its shape is altered dynamically for breathing, eating or vocalization. The pharynx is dilated to maintain airway patency for breathing, but is constricted to push the food bolus down to the esophagus for swallowing.

2.1. Pharynx for breathing

The muscle activities of the soft palate, tongue and pharyngeal wall are critical to maintaining pharyngeal airway patency for proper ventilation and gas exchange [7–15]. Pharyngeal muscles counteract negative transmural air pressure that tends to collapse the airway during inspiration. In obstructive sleep apnea, the activities of pharyngeal muscle activities are suppressed during sleep, allowing the pharyngeal airway to collapse during inspiration. There are extensive studies investigating control mechanisms of pharyngeal muscles and their role in the pathogenesis of breathing disorders [15,16].

The genioglossus, which is the main muscle for tongue protrusion, has a critical role in controlling pharyngeal airway patency. It is tonically active to maintain tongue position, and is phasically active to counteract intraluminal negative pressure during inspiration [11]. Therefore, the majority of the studies related to obstructive sleep apnea have focused on motor control of the genioglossus in animals or humans [15,16]. Several studies have also reported muscle activities of the other extrinsic tongue (hyoglossus or styloglossus) muscles or the intrinsic tongue muscles [12,13].

The soft palate has an important role in determining the route of respiration [9]. During nasal breathing, the soft palate is lowered and apposed to the tongue, dilating the velopharyngeal isthmus (retro-palatal airway) [17]. During oral breathing, in contrast, the soft palate elevates to open the faucae, separating the nasal cavity from the pharyngeal airway [18]. Complex activities of several palatal muscles determine the position of the palate for the route of respiration. The two main muscles for determining palatal position are the levator veli palatini and the palatoglossus. Both muscles are active during oral and nasal breathing. However, the levator palatini is more active during oral breathing and the palatoglossus during nasal breathing [19].

2.2. Pharynx for mastication and swallowing

Food processing occurs in the oral cavity and the chewed food bolus is transported to the oropharyngeal surface of the tongue and the valleculae during mastication. Thus, the pharynx becomes the space for bolus aggregation prior to the pharyngeal swallow. Pharyngeal bolus aggregation continues for a few seconds in healthy individuals eating solid food while breathing continues [4]. During this period of bolus aggregation, the pharyngeal space is shared by feeding and breathing.

During swallowing, the pharynx is used only for the food passage and is completely separated from the airway in healthy individuals. Velopharyngeal closure separates the nasal cavity from the pharynx, and laryngeal closure, including glottal closure, arytenoid adduction, and epiglottal folding, seals the lower airway. The backward movement of the tongue and gradual progressive contraction of the pharyngeal wall contraction (starting at the level of the soft palate and
proceeding downward) squeeze the food bolus into the esophagus through the upper esophageal sphincter.

3. A sequence from mastication to swallowing

3.1. Process model of feeding

The normal swallow in humans is previously described with a four-stage sequential model. In this model, the swallowing process was depicted as having oral preparatory, oral propulsive, pharyngeal, and esophageal stages based primarily on the location of the bolus in the food pathway [20,21] (Fig. 1). According to this model, the four stages progress sequentially, with minimal temporal overlap among stages. The swallowing process may be appropriately described as a five-stage process adding pre-oral (anticipatory) stage in case of considering clinical diagnosis and treatment of dysphagia [22]. Pre-oral stage accounts for pre-oral motor, cognitive, psychosocial and somat aesthetic factors. These factors have significant influence on the following stages, and impairment of the pre-oral stage has significant influence on oral or oropharyngeal dysphagia.

Mastication was regarded as a part of oral preparatory stage in the four-stage sequential model. During the oral preparatory stage, the food was thought to be retained in the oral cavity by closure of the lips anteriorly and the faucial isthmus posteriorly. Firm contact between the soft palate and the posterior surface of the tongue was believed necessary to prevent premature leakage of the food into the pharynx and prevent aspiration prior to the swallow [21].

The Process Model of Feeding provides an alternative description for mastication and swallowing in which triturated food is propelled through the fauces for bolus formation in the oropharynx (including the valleculae) during chewing. The Process Model has its origin in studies of mammalian feeding [6,23—27] and was later adapted to feeding in humans [1]. When eating solid food, the food is first transported to the occlusal surfaces of the postcanine dentition (stage I transport, Fig. 1). Then, the food is reduced in size and lubricated with saliva (food processing). Triturated food is transported to the oropharynx (stage II transport) and collects there (bolus aggregation) until swallow onset. Food processing continues during stage II transport and bolus aggregation in the oropharynx. Thus, the oral preparatory phase (food processing) and oral propulsive phase (stage II transport and bolus aggregation) are can overlap in time (Fig. 1). This is a significant difference of the process model from the conventional model of swallowing.

After ingestion and stage I transport, the food is processed until it is ready for swallowing. During processing, food particles are reduced in size and softened by mastication and mixed with saliva to optimize bolus consistency for swallowing. Cyclic jaw movement is temporo-spatially coordinated with the movements of the tongue, cheek, and soft palate during food processing [28—31].

With aging, there is an increase in the number of chewing cycles and the myoelectric activity of the jaw adductor musculature during mastication [32,33]. These factors result in increased mastication time. But despite the increase in mastication time, bolus size at the time of swallow onset is larger in the elderly than in the young, primarily because of the decrease in masticatory function.

Figure 1 Four sequential model and process model are illustrated in diagrams showing progression from left to right, and aligning the common elements of the two models. (A) In the conventional sequential model, the four stages have minimum overlap so that oral propulsive stage starts after oral preparatory stage is completed. (B) In the Process Model, food processing (in the oral cavity) and bolus aggregation (in the pharynx) can occur at the same time. After food is ingested into the mouth, it is carried to the post-canine teeth for mastication (stage I transport). The food is reduced in size by chewing and mixed with saliva until it is ready to swallow (Food Processing). A portion of the chewed food is propelled into the oropharynx (stage II transport, ST II), where the bolus gradually accumulates while food processing continues in the mouth. Subsequent stage II transport cycles bring additional food to the oropharynx, and the bolus gradually accumulates there. Arrows indicate stage II transport cycles. Pharyngeal and esophageal stages have essentially the same mechanisms in the two models.

Figure 2 Vertical movement of the jaw, hyoid bone, and soft palate over time while eating a piece of banana. This is an actual recording of a healthy adult volunteer. Motions were measured with videofluorography and an image analysis system. Movement towards the top of the figure is upwards. Rhythmic movements of the soft palate and hyoid bone are temporally associated with cyclic jaw movement. (Source: Ref. [34])
Tongue movement is temporally linked with cyclic jaw movement in food processing [28]. During chewing, the tongue (pushing laterally) and the cheek (pushing medially) reposition food on the occlusal surfaces before each closing stroke of the teeth [29]. The tongue moves anteroposteriorly, mediolaterally, and rotates on its three axes during chewing. Those tongue movements can carry all or part of the food piece to the opposite side of the mouth during food processing, thus reversing the working and balancing sides. Bilateral chewing is also seen frequently in healthy adults [29].

The soft palate moves cyclically during feeding, and this movement is temporally (but not mechanically) linked to jaw movement [30] (Fig. 2). The soft palate always elevates during pharyngeal swallowing, and often elevates during processing and stage II transport. However, the temporal relationships between jaw and soft palate movements during food processing are totally different from the relationships during swallowing [34]. During processing, the soft palate moves upward as the jaw opens and downward as the jaw closes (Fig. 3). During swallowing, however, the soft palate elevates after the jaw is closed and (for swallows intercalated during chewing) descends during jaw opening (Fig. 3). The movement of palatal movement varies greatly among individuals but the timing of palatal movement relative to jaw movement is highly consistent [30]. Rhythmic movements of the soft palate and tongue open the fauces during food processing to provide open communication between the oral cavity and pharynx.

When a portion of the food is suitable for swallowing, the triturated food is segregated from the particles on the occlusal surface and gathered on the dorsal surface of the tongue. The food is propelled back through the fauces to the oropharynx by the tongue squeezing it back along the palate. This propulsion of the food is called stage II transport [4,35]. Stage II transport is primarily driven by the tongue, and does not require gravity, though it is assisted by gravity in the upright position [3,36]. During stage II transport cycles, the tongue squeezes the food bolus back along the palate during jaw opening, and the palate elevates briefly after that squeeze-back action [30] (Fig. 4).

Stage II transport occurs intermittently during food processing [30] but the frequency of stage II transport cycles increases toward the swallow. The transported food accumulates on the oropharyngeal surface of the tongue and the valleculae until swallow initiation. Chewing continues, and the bolus in the oropharynx is increased incrementally by subsequent stage II transport cycles. The duration of bolus aggregation in the oropharynx ranges from a fraction of a second to about ten seconds, and has substantial inter-individual variation [4].

The relationships among food transport, bolus aggregation, and swallow initiation are modified by the physical character-
istics of the food and by coupling these activities with mastication [2—4]. When drinking liquid, the bolus is commonly held in the oral cavity until just before the initiation of the pharyngeal swallow; this is believed to be important for preventing aspiration of the liquid. When eating solid food, however, food is propelled to the oropharynx where it accumulates and bolus is formed prior to swallowing. Saitoh et al. [3] studied normal subjects eating a complex food containing both liquid and solid phases. They reported that the leading edge (liquid component) of the food often reached the hypopharynx before swallow initiation (Fig. 5). Gravity had a significant impact on the position of the leading edge of the food at swallow initiation with these two-phase foods. When eating in a facedown posture (upper body and head parallel to the ground), the leading edge of the food never entered the hypopharynx before swallow initiation.

4. Coordination between breathing and swallowing

4.1. Airway protective mechanism during swallowing

Safe bolus passage through the pharynx without tracheal aspiration is critical to human swallowing. Thus, swallowing has two essential physiologic aspects: (1) passage of food from the oral cavity to the stomach and (2) airway protection to prevent contamination of the trachea, bronchi, and lungs. There are several airway protective mechanisms preventing aspiration of foreign materials into the trachea before, during, and after swallowing.

There are three gate keepers to prevent tracheopulmonary aspiration: the epiglottis, arytenoids, and vocal folds. There is fine temporal coordination among these structures, resulting in laryngeal closure that starts at the bottom and progresses upward. First in sequence is adduction of the true vocal folds. This closes the glottis (space between the vocal folds). Next is closure of the laryngeal vestibule. The false vocal folds adduct and the arytenoid cartilages adduct and tilt forward to contact the base of the epiglottis prior to opening of the UES [37,38]. The epiglottis is the most superficial shield for lower airway protection. The mechanism of posterior epiglottic tilting in human swallowing remains unclear, but is probably related to hyo-laryngeal elevation, pharyngeal constriction, bolus movement, and tongue base retraction [39]. During swallowing, the hyoid bone and larynx are pulled upward and forward by contraction of the suprahyoid muscles and thyrohyoid muscle. This displacement tucks the larynx under the base of the tongue, helping the epiglottis tilting backward to seal the laryngeal vestibule (Fig. 6).
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The vocal folds closure reflex occurs not only in swallowing but also in belching and esophageal distention [40,41]. During belching, the vocal folds close and the arytenoids adduct before the UES opening [40]. These reflexes may also play an important role in preventing aspiration of the materials regurgitated to the pharynx after gastro-esophageal reflux.

4.2. Swallowing and respiratory phase

Swallowing and respiration have tight temporal coordination in adult humans. A number of studies, using various measurement systems and different food consistencies, confirm that swallowing usually occurs during expiration. Martin-Harris [42] presented an excellent summary table in her online review of studies on temporal coordination of breathing and swallowing in adult humans. In those studies, respiratory inductive plethysmography and/or nasal air pressure manometry was used to monitor respiratory phase (inspiration vs. expiration). Physiologic events during swallowing were analyzed with indirect (submental EMG or swallow sounds), or direct visualization (videofluorography or videodendoscopy).

In adult humans, swallowing usually starts during the expiratory phase of breathing, and respiration resumes with continued expiration after swallowing. Many studies investigate the temporal coordination between breathing and swallowing of a liquid bolus. The predominant respiration-swallowing pattern in adult humans is the “exhale—swallow—exhale” pattern (67–79%), followed by “inhale—swallow—exhale” pattern (18–21%) [43–45]. The “exhale—swallow—inhale” and “inhale—swallow—inhale” patterns occur rarely in healthy adults. The resumption with expiration is regarded as an airway protective mechanism as it can prevent inhalation of residual material left in the pharynx after swallowing [46].

The swallow respiratory temporal coordination varies with the conditions of swallowing, including method of ingestion, body position, and food consistency. When performing sequential swallows while drinking from a cup, respiration can resume in inspiration [47]. When drinking liquids while positioned down on hands and knees, swallow onset is more likely to occur during early expiration while swallows in upright position tend to occur late in the expiratory phase [48]. With eating solid food, temporal coordination persists with the "exhale—swallow—exhale" relationships [49–51].

Swallow-respiratory coordination varies across the human lifespan. The temporal coordination in infants is different from that in adults. In infants, the temporal pattern of respiratory phase and swallowing is more variable, and swallows are more likely to occur during inspiration [52–54]. This may be due to anatomical differences between infants and adults and/or maturation of the neural control mechanisms. In infants, the larynx is in positioned higher in the neck, posterior to the oral cavity. It is opened to the nasopharynx, sealed off from the food pathway (between swallows) by contact between the soft palate and epiglottis. The larynx descends in the neck during infancy [55], and the temporal coordination between breathing and swallowing shifts to “exhale—swallow—exhale” relationships [56–58].

Swallow-respiratory coordination is altered in the elderly as well. Respiratory patterns are characterized by increased incidence of inspiration both before and after the swallow [46,59–62]. Swallow-respiratory coordination is further altered by disease. Swallows occur more frequently during inspiration in individuals with cerebrovascular disease, Parkinson’s disease and other neurological diseases [60,63–66]. This occurrence of swallowing during inspiration could be a causal factor in the high incidence of aspiration pneumonia in these diseases [67,68].

4.3. Pause in breathing during swallowing

Breathing ceases briefly during swallowing. The pause in breathing is due to inhibition of respiration at neural control centers in the brainstem, and not simply due to closure of the upper airway [49,69,70]. Indeed, inhibition of breathing during swallowing persists after endotracheal intubation or laryngectomy (in which the airway and foodway are separated anatomically [70,71]). The onset of the pause in breathing for swallowing is approximately synchronous initiation of bulbus propulsion in the oral cavity during a swallow of a single liquid bolus [59]. The duration of respiratory pause is 0.5–1.5 s in healthy adults [43,45,69]. The effect of bolus volume on duration of respiratory pause is still controversial. Some studies report an increase in duration with bolus volume increase [61,72]. Hiss et al. suggested that this prolongation is due to earlier onset of swallowing apnea with larger volume [72]. The other studies reported no difference in swallowing apnea duration among different bolus volumes [73,74]. The duration of the pause in breathing for swallowing is prolonged with aging [59].

When eating solid foods, the timing and duration of the pause in breathing are highly variable [49,50,75,76]. The pause in breathing often begins substantially before the swallow, and the swallow occurs during these extended
pauses [49,50]. This increases respiratory cycle duration substantially [50,51,73]. Matsuo et al. reported that the prolongation of the respiratory cycle duration exceeds the duration of the swallow itself [50]. They suggested that this prolongation was due, in part, to the period of pre-swallow bolus aggregation in the pharynx, however, it could begin during food processing, before the onset of stage II transport.

5. Coordination between breathing and mastication

It was long believed that the oral cavity is separated from the pharynx during food processing by posterior tongue-palate contact that closes the fauces until the food is ready for swallowing. More recent studies reveal that the fauces are typically open during food processing and triturated food is propelled to the oropharynx (stage II transport) well before swallow initiation. These studies indicate that the food accumulating in the oropharynx is located in the path of respiratory airflow during mastication. Respiration and mastication must be controlled so as to prevent aspiration during this period of bolus aggregation given the overlapping anatomy of airway and foodway.

5.1. Change of respiratory cycle duration

Eating solid food alters the respiratory rhythm. The rhythm is perturbed with onset of mastication. Respiratory frequency increases during mastication, but decreases with swallowing [49,50,77] (Fig. 7). Fontana et al. reported that total airway resistance increases during mastication, suggesting a reduction in upper airway patency during mastication due to the activities of the masticatory muscles. Prolonged periods of respiratory pause associated with feeding are reported in normal individuals [49,50,75] and several laryngectomized individuals [76]. Those results may represent an exaggerated physiological response to the presence of food in the oral cavity and pharynx.

5.2. Air movement during mastication

During food processing in the mouth, cyclical movements of the soft palate and tongue moves are temporally linked with masticatory jaw movement [28,30,34]. This opens the fauces during food processing, and provides a route for communication between the oral cavity and nasal cavity through the pharynx. While eating of solid food, breathing is through the nose, not the mouth, since the oral cavity is used for food processing and the lips are sealed to prevent the food from escaping anteriorly [50]. Nasal air manometry captures the changes in air pressure associated with breathing. It also demonstrates oscillations in nasal air pressure associated with masticatory jaw movement [75,78,79]: nasal air pressure is positive during jaw closing and negative (relative to atmospheric pressure) during jaw opening. Finding from these studies suggest that jaw closing pumps the air from the mouth to the nasal cavity, through the pharynx. Air movement associated with masticatory jaw movement may also deliver aroma of the chewed food to nasal chemoreceptors [79].

5.3. Airway protection during bolus formation in the pharynx

Triturated food is aggregated in the oropharynx for a period of time before swallow, while the larynx is open. The presence of the food in the pharynx can present a risk for pre-swallow aspiration, if respiration continues and the airway remains open. Indeed, air can be inhaled through the pharyngeal airway while food is but a few millimeters from the laryngeal aditus. The mechanisms which prevent aspiration during the period of bolus aggregation in the oropharynx are
not well understood. Palmer and his colleagues have investigated the relationship between the location and timing of pharyngeal bolus aggregation and breathing pattern [50,75]. It is well known that there is a pause in breathing during the pharyngeal swallow, as discussed above. A preliminary investigation by Palmer and Hiiemae [75], using nasal air pressure manometry, suggested that the period of respiratory inhibition may be longer than the swallow itself, to incorporate the pre-swallow period of bolus aggregation and that respiration is inhibited during bolus aggregation. They conducted further investigation of breathing patterns during the mastication, aggregation and swallowing, using both nasal manometry and respiratory plethysmography [50]. Matsuo et al. found that there can be inspiration, expiration or a pause in breathing during bolus aggregation, and in some cases there are frequently multiple respiratory cycles during bolus aggregation. These findings suggested that the presence of the food in the valleculae did not directly influence control of respiration.

Several mechanisms for airway protection during bolus aggregation have been proposed [2,80]. Dua et al. [2] reported that the vocal folds close briefly when the bolus is propelled to the pharynx. They suggested that this brief adduction of the vocal folds may help to prevent aspiration before swallowing. Another proposal is the optimization model for mastication and swallowing by Prinz and Lucas [80]. They hypothesize that there is an optimal cohesiveness of the food bolus for swallowing that depends on the size of particles and the quantity of saliva. During food processing, food particles are reduced in size by mastication and mixed with saliva. Salivation lubricates the food particles to provide optimized cohesiveness for bolus formation in the pharynx. Accordingly, they suggested that the resulting bolus has optimized particle size and cohesiveness for swallowing. This enables the bolus to remain stick together rather than falling apart during bolus aggregation and swallowing. They also suggested that if swallowing is delayed, excessive saliva can flood the bolus, separating particles and reducing cohesion.

Palmer and his colleagues revealed that stage II transport may be inhibited volitionally during feeding [81]. When healthy subjects are instructed to chew food and hold it in the mouth until they think it is ready for swallowing, stage II transport is delayed, and transport to the valleculae inhibited. Volition alters swallow initiation in both timing of swallowing and mastication, and in the mechanisms for pre-swallow bolus aggregation and breathing pattern [50,75]. Matsuo et al. found that there can be inspiration, expiration or a pause in breathing during bolus aggregation, and in some cases there are frequently multiple respiratory cycles during bolus aggregation. These findings suggested that the presence of the food in the valleculae did not directly influence control of respiration. Delayed swallow initiation or premature leakage of the food into the foodway before swallowing is regarded as a frequent characteristic of abnormal swallowing [21,82,83]. However, delayed swallow initiation is not simply defined, since pre-swallow bolus entry into the pharynx occurs in healthy individuals drinking liquids [84—86] or eating solid food [1—3]. The presence of the food in the pharynx before swallowing is not necessarily abnormal, but it can increase risk of aspiration in dysphagic individuals with poor airway protection. Further investigations are needed to determine the significance of food remaining in the pharynx for an extended period before swallowing in individuals with dysphagia.

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