AD-A270 208 N PAGE

Form Approved
OMB No. 0704-0188

1. AGENCY USE ONLY (Leave blank)

2. REPORT DATE
1993

3. REPORT TYPE AND DATES COVERED
THESIS/~~DISSERTATI~~ON

4. TITLE AND SUBTITLE
Movement of the Epiglottis in Mammals

5. FUNDING NUMBERS
1

6. AUTHOR(S)
James E. Larson

7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES)
AFIT Student Attending: Univ of Washington

8. PERFORMING ORGANIZATION REPORT NUMBER
AFIT/CI/CIA- 93-133

9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)
DEPARTMENT OF THE AIR FORCE
AFIT/CI
2950 P STREET
WRIGHT-PATTERSON AFB OH 45433-7765

10. SPONSORING/MONITORING AGENCY REPORT NUMBER

11. SUPPLEMENTARY NOTES

12a. DISTRIBUTION/AVAILABILITY STATEMENT
Approved for Public Release IAW 190-1
Distribution Unlimited
MICHAEL M. BRICKER, SMSgt, USAF
Chief Administration

12b. DISTRIBUTION CODE

13. ABSTRACT (Maximum 200 words)

DTIC
ELECTE
OCT 06 1993
S A D

93-23216

40pg

93 10 4 048

14. SUBJECT TERMS

15. NUMBER OF PAGES
33

16. PRICE CODE

17. SECURITY CLASSIFICATION OF REPORT

18. SECURITY CLASSIFICATION OF THIS PAGE

19. SECURITY CLASSIFICATION OF ABSTRACT

20. LIMITATION OF ABSTRACT

NSN 7540-01-280-5500

Standard Form 298 (Rev. 2-89)
Prescribed by ANSI Std. Z39-18
298-102

MOVEMENT OF THE EPIGLOTTIS IN MAMMALS

by

James E. Larson D.D.S.

A *thesis submitted in partial* fulfillment
of the requirements for the degree of

MASTER OF SCIENCE IN DENTISTRY

UNIVERSITY OF WASHINGTON

1993

Approved by ________________________________
(Chairperson of Research Committee)

Department ____________ School of Dentistry ____________
(Departmental Faculty sponsoring candidate)

Date ________________________________

Master's Thesis

In presenting this thesis in partial fulfillment of the requirements for an advanced degree at the University of Washington, I agree that the Library shall make it freely available for inspection. I further agree that permission for extensive copying of this thesis is *allowable only for scholarly* purposes, consistent with "fair use" as prescribed in the U.S. Copyright Law. Any other reproduction for any purposes or by any means shall not be allowed without written permission.

Signature ______________________

Date ___________________________

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGMENTS

I would like to particularly thank the chairperson of my research committee, Dr. Sue Herring for her extensive advice, guidance and encouragement. Her dedication to her work will always be an inspiration to me. My thanks also are extended to the other members of my committee, Dr. Peter Shapiro, Dr. Doug Ramsay and Dr Lars Hollender. Dr. Raymond Fink was an unofficial member of my committee. I appreciated his advice and wisdom.

Trish Emry put in many hours in helping around the lab, especially in pig training and for that I am very grateful. Thanks are also extended to David Wright for his computer help and aid with statistics. Jim Clark helped with my illustrations and photography for which I am very appreciative. Frank “Rusty” Starr performed all of the cinefluoroscopy which was at the heart of this study.

I am thankful also to the alumni who funded this study and whose dedication and guidance will be with me always.

My classmates offered much valuable advice and encouraged me every step of the way along our journey. It was an honor and a total pleasure to be associated with them.

To my wife, Mary, and to my sons Tim, Jon, Jeff, Ethan, Ben and Eric goes all of my love forever. I do everything thinking of you.

INTRODUCTION

The Problem

The spatial positioning of the human larynx and epiglottis relative to the pharynx is uniquely different from that found in other mammals. However, it has not been clearly established whether these anatomical differences reflect functional differences. The epiglottis of the adult human moves downward during swallowing movements (Mosher, 1927; Welin, 1939; Johnstone, 1942; Saunders et al., 1951; Rushmer and Henderson, 1951; Fink, 1956; Ardran and Kemp, 1967), presumably to protect the airway (Fig. 1a,b), but such an action has been disputed in human infants and other mammals.

Position of the Epiglottis

From as early as 21 weeks in utero (Magriples and Laitman, 1986) to approximately 4 to 6 months of age (Sasaki et al., 1977) or 6 years of age (Crelin, 1987) the epiglottis of human infants makes contact with the soft palate because of the superior location of the entire hyolaryngeal apparatus (Fig. 1c). Thus, until at least six months of age and perhaps up to six years, humans are obligate nasal breathers. The age disparity between the cited studies is large and suggests that preserved specimens may not always reflect in vivo morphology. Nevertheless, in the adult human the epiglottis never touches the soft palate and mature humans are quite capable of nasal and/or oral breathing.

The contrast between infant and adult epiglottic position has been viewed within the context of human evolution by Lieberman and colleagues (1972) and Laitman (1982), who argued from cranial base anatomy that Neanderthals had contact of the epiglottis and soft palate. Thus, they speculated that early men were obligate nasal breathers, like infants, and had a heightened sense of smell. While not universally accepted (DuBrul, 1976), these findings have had broad currency in linguistic and anthropological circles (e.g., Bickerton, 1990; Ross, 1991).

Negus (1949), who did the classic, descriptive work on the larynx, noted that some reptiles and birds have an epiglottis but the relative size is small compared to mammals. In mammals a prominent epiglottis is the rule. Negus extrapolated from his dissections to live animals and concluded that, except in mature humans, the epiglottis touches or overlaps the posterior or the anterior surface of the soft palate during breathing. According to Negus, this would serve to enforce nasal breathing and thus heighten the sense of smell, the same advantages that Laitman ascribed to Neanderthals. Among land mammals, the ungulates represent an extreme condition in which a large epiglottis extends well into the nasopharynx on the posterior side of the soft palate. Negus noted that this arrangement would promote uninterrupted olfaction and breathing even during feeding, an advantage for these prey animals which must spend large amounts of time consuming their non-nutritious diets.

Although Negus' comprehensive anatomical studies have been influential in the anthropological community, his physiological deductions have not proved reliable. For example, Negus postulated that in dogs the anterior-lying epiglottis acts as a two-way valve to direct air through the nose during inhalation and through the mouth during exhalation, facilitating temperature regulation. However, Biewener and associates found that the in vivo position of the epiglottis in dogs varies and that it actually lies posterior to the soft palate during many activities (1985). This study points out the limitations of making conjectures based on anatomic study alone and raises doubts about other commonly accepted tenets of laryngeal function.

Role of Epiglottis During Swallowing

A.The Adult Human

While epiglottic anatomy has rarely been debated, this has not been the case for epiglottic movement during swallowing. Magendie (1816, cited by Negus, 1949) exemplified the prevailing view of his time, which was that the epiglottis folded down, lid-like, over the laryngeal inlet during swallowing. In 1892 Stuart, in making observations on a patient with a lateral pharyngostomy, reported that the epiglottis remained upright during swallowing movements (cited by Negus, 1949). (In retrospect, this could have been a case of paralysis such as those reported by Ekberg [1983]). This incident, along with the anatomical data, was used as support by Negus (1949) for his contention that the epiglottis of man and other mammals remained upright and respiration continued during the swallowing of liquid or semi-solid food.

The bulk of evidence, however, contradicts the theory that the human epiglottis remains upright during swallowing. Using radiography, Mosher (1927) reported that the epiglottis "does act as a cover for the larynx in swallowing." His results have been confirmed in similar studies by Welin (1939), Johnstone (1942), Saunders et al. (1951), Rushmer and Henderson (1951), Ramsay (1955), Fink (1956), Ardran and Kemp (1967), and Ekberg and Sigurjonsson (1982), all concluding that the human epiglottis does indeed move downward to cover the laryngeal inlet at least partially during swallowing.

While the downward movement of the adult human epiglottis during swallowing is no longer disputed, the significance of the movements has been challenged (Crelin, 1987). One argument used to support depiction of the epiglottis as vestigial is the fact that after removal of the epiglottis people can swallow without difficulty (Laitman, 1977, 1980). However, the test of whether an organ is vestigial is not whether the organism can adapt to its loss. Ardran (1952) described swallowing patterns in individuals missing all or part of their epiglottis and noted many adaptations in the swallowing mechanism and the considerable disadvantage resulting from these compensations.

B.The Human Infant

Following Negus, a number of workers contend that, in contrast to adult humans, human infants can swallow (at least liquids) and breathe simultaneously, a claim also made for non-human mammals (Crelin, 1987; Magriples and Laitman, 1987). The major functional evidence cited in support of this contention is a well-known radiographic study of bottle feeding by Ardran et al. (1958). However, the citation is typically incomplete. While Ardran et al. did report that the epiglottis is erect when the bolus begins its passage into the pharynx, they also found that the epiglottis was turned down and the larynx closed as the bulk of the bolus moved into the pharynx. Indeed, they explicitly suggested that Negus' hypothesis of simultaneous breathing and swallowing was incorrect (p. 21).

Bosma (1986) illustrated but did not discuss drawings depicting cineradiography of suckle feeding and swallowing in infants. Relatively late in swallowing as the milk descends past the larynx, the epiglottis is shown moving to appose the raised arytenoids. These observations appear to be consistent with those of Ardran et al. (1958) and indicate that the combined movements of the epiglottis and arytenoids effectively obturate the laryngeal opening during swallowing.

In addition, the simultaneous nature of breathing and swallowing in the human infant has been disproved by non-radiographic studies. Wilson et al. (1981) found that non-feeding swallows in infants were accompanied by cessation of breathing for an average of 1 sec. A variety of physiological and imaging techniques have been used to show that feeding swallows cause temporary apnea (Kenney et al., 1989; Koening et al., 1990; Selley et al., 1990). Thus, swallowing and breathing never co-occur. However, techniques that do not involve visualization of the epiglottis are incapable of showing whether epiglottic movement is involved in the apnea, or indeed whether the cause of the apnea is a physical one (i.e. caused by blockage of the airway).

C. Other Mammals

The interpretation of the infant epiglottis as immobile was in large part based on the assumption that this was the primitive mammalian state. Negus did not view the mammalian epiglottis as playing any role in protecting the glottis during swallowing. In herbivores, particularly, he proposed that the upright epiglottis directs the semi-liquid bolus around its sides and to the esophagus by way of the "lateral food channels" with no interruption of breathing (Negus, 1949). In carnivores, which tend to swallow their food whole, or in herbivores swallowing a large solid bolus, the epiglottis might be forced downward over the glottis by pressure of the bolus but this was a secondary, passive act and not protective of the glottis.

Several radiographic studies have addressed the matter, but with conflicting results. Ardran et al. (1958) examined suckling in lambs and kid goats and reported epiglottic downturning after the initiation of swallowing. In a study on pigs Herring and Scapino (1973) saw the bolus flowing over the top of the lowered epiglottis. Unfortunately, neither of these studies employed radiopaque markers, so the findings are not definitive. Other studies have avoided a detailed description. Fink and Demarest (1978) noted epiglottic movements during laryngoscopy in orangutans and dogs but did not describe them. Laitman and colleagues (1977) used tantalum clips in cineradiographic observations on a young monkey. They reported that, "During deglutition the epiglottis and soft palate were also seen to be in overlapping contact" but added that a "momentary separation frequently occurred that was most often related to the density of the liquid being swallowed." Even while drinking water the separation frequently occurred. Thus, their conclusion that breathing and swallowing were simultaneous seems somewhat equivocal. Biewener et al. (1985) found that respiration ceased entirely in dogs during eating and drinking and mentioned epiglottic movements during swallowing but did not describe these movements.

As in the case of human infants, non-radiographic studies have confirmed that respiration and swallowing do not co-occur (McFarland and Lund, 1993, and literature cited therein). However, the role of the epiglottis in the apnea is unknown.

Purpose

The *above literature review* establishes that there is no evidence for simultaneous breathing and swallowing in any species. However, the role of the epiglottis is unclear. The studies purporting to see downturning (Ardran et al., 1958; Fink, 1978; Herring and Scapino, 1973) did not employ radiopaque markers, casting some doubt on their validity. Further, no published study has quantified swallowing movements to an extent that would allow an assessment of the importance of bolus size or density. Therefore, our purpose is to use radiopaque markers to provide a detailed description of epiglottic movement in two mammalian species representing expected extremes of epiglottic function. Specifically, we ask whether the epiglottis is lowered to close the airway during swallowing. An ungulate (pig) and a carnivore (ferret) served to illustrate the typical conditions found in these groups.

MATERIALS AND METHODS

The sample consisted of three Hanford miniature pigs (Sus scrofa, Charles River Labs, Wilmington, MA), and three ferrets (Mustela putorius furo, Marshall Farms, North Rose, NY). The pigs were weaned female juveniles weighing between 25 - 35 kg. and the ferrets were adult males weighing between 1.25 and 2.0 kg.

The pigs were trained to eat pig chow pellets, semisolid chow mixed with milk substitute and liquid milk substitute alone. One of the pigs was trained to eat both solid and liquid food mixed with barium sulfate. The ferrets were fed ferret chow pellets, softer ground turkey and water. Two of the ferrets were trained to eat ground turkey mixed with barium sulfate. The pigs were trained to eat from a feeding stand, and the ferrets were trained to eat from a radiolucent feeding box.

Epiglottic markers consisted of U-shaped clips which were compressed with a special instrument. The pig clips were formed from 0.8 mm stainless steel and were approximately 4.0 mm x 6.0 mm before compression, whereas the ferret clips were approximately 4.0 mm x 4.0 mm stock tantalum hemoclips. The markers were compressed onto the free edge of the epiglottis near the median plane.

The soft palate markers consisted of 3-4 mm sections of either 0.8 mm round or 0.5 mm x 0.6 mm rectangular stainless steel wire. These sections of wire were injected into the submucosal tissue of the soft palate by being placed into the lumen of a hypodermic needle and then forced out with a wire attached to the plunger of the syringe. An attempt was made to place the marker in the median plane as close to the free margin of the soft palate as possible.

For marker placement pigs were anesthetized using 1- 3% halothane in a 50-50 mixture of nitrous oxide and oxygen administered by a mask. The mask was removed for marker placement, which was aided by laryngoscopy. Ferrets were anesthetized with Ketamine (25 mg/kg IM) and Xylazine (1 mg/kg IM). Atropine (0.10 mg/kg IM) was sometimes used to control salivary secretions. This regimen produced a light stage of anesthesia for approximately 30 minutes during which laryngoscopy allowed marker placement. The ferrets were radiographed after clip placement to verify proper positioning.

After a recovery period of at least 24 hours, during which time normal eating patterns were observed to have returned, the animals were observed fluoroscopically while feeding. A portable Siemens fluoroscopy unit (30 frames/sec) coupled to a high resolution Panasonic monitor and video images were recorded with a time overlay. A total of 125 swallows for the pigs and 60 swallows for the ferrets were taped. At the conclusion of the experiments the animals were euthanized, and dissections were made to clarify anatomical relationships and document marker position.

Video images were examined at normal speed, in slow motion and frame by frame. Epiglottic movement was divided into three time intervals for analysis. The first time interval was the descent time of the epiglottis, defined as the frame just prior to initiation of the swallow to the frame when the epiglottis marker first became visible in the downward position. The second interval, the time spent by the epiglottis in the downward position, was taken from the first frame in this position to the frame just prior to its ascent. The third interval, the ascent time, was taken from this last frame to the first frame in which the epiglottis was erect.

Means and standard deviations were calculated for the time intervals observed. Tests for significance were performed using the non-parametric Wilcoxon-Mann-Whitney test for independent samples corrected for ties.

The markers and anatomical landmarks were digitized and plotted (Peak 2D and Peak 5 programs, Peak Performance Technologies, Englewood, CO). In the pig, the movements of the soft palate and epiglottic markers were referenced against the most ventral point on the ventral arch of the atlas and the most caudal, ventral point on the body of C-2 (Fig. 2). These reference points eliminated the effects of neck movements. In the ferret the smaller size of the head permitted the use of skull points as references, the most posterior, superior point of the occipital bone and the most anterior point of the nasal bone (Fig. 3, S1 and S2). Photographs were made of individual frames to provide a schematic overview of laryngeal anatomy and to demonstrate the gross movements of the swallowing cycle.

RESULTS

Anatomy

In contrast to the human condition, in which the epiglottic cartilage lies well below the level of the dorsum of the tongue (Fig. 1a), in both the pig and ferret (Figs. 2,3) the entire epiglottic cartilage lay well above this level. In the pig the epiglottis projected cylindrically from the superior aspect of the larynx; its rounded free margin lay for more than a centimeter of its length upon the dorsal surface of the soft palate. This was observed radiographically in living animals as well as in cadaver dissections. During marker placement the soft palate had to be pushed far superiorly to allow the epiglottis to move from the nasal cavity to the oral cavity. Its normal position is thus intra-narial as in other ungulates. In the ferret the free margin of the epiglottis was pointed, and as in other carnivores, its normal posture was intra-oral rather than intranarial. The nasopharyngeal orifice was only 2 - 3mm in diameter (Fig. 3). Although it would be physically possible, the epiglottis was never observed to project through this orifice.

In the human, pig and ferret the epiglottis is closely related to the larynx and particularly to the hyoid bone. Pigs and ferrets have hyo-epiglottic muscles in addition to hyoepiglottic ligaments (Sisson and Grossman, 1938). Presumably, movements in these structures would be transmitted to the epiglottis.

Fluoroscopy - Technical Considerations

Sequences selected for analysis were those with minimal head movement and good outlines of all bony structures, as well as faint outlines of the epiglottis, thyroid cartilage, tongue, and soft palate. Structures were generally easier to visualize on the much larger pig. At rest and during chewing, all markers were visible except the soft palate marker in the ferret which was rarely visible. Hence, we did not analyze the movements of this marker.

Movements

In both species the formation of a bolus from solid or semi-solid food involved various degrees of mastication. For liquids, the animals either lapped (ferret) or sucked (pigs) to form a bolus prior to swallowing. The epiglottis, with the rest of the hyolaryngeal apparatus, moved in regular cycles during chewing or drinking.

Bolus formation was an unvarying phenomenon for liquids, *semisolids and solids. In the pig* boluses of food were formed in a space bounded by the posterior dorsum of the tongue, the anterior surface of the soft palate and the anterior surface of the epiglottis. The area of bolus formation was similar in the ferret but the exact boundaries of the space could not be well defined.

Swallowing in both species commenced with a downward movement of the bolus and the simultaneous unmistakable descent of the epiglottis (Figs. 4-6). There was no difference in the nature of epiglottic movement for foods of different consistencies. The upright epiglottis swung through an arc of greater than 90 degrees as it descended. Continuity with the soft palate was lost.

Soft palate movements (observed only in pig) were less impressive (Fig. 5). During the descent of the epiglottis and passage of the bolus, there was a small dorsal movement of the free edge of the soft palate. After the bolus had passed, the soft palate returned ventrally, occupying the space vacated by the bolus. The return of the soft palate was typically one frame (0.03 sec) delayed relative to the ascent of the epiglottis. Despite the minor movement of the marker in the free edge of the soft palate, the nasopharynx in the pig appeared to be occluded during swallowing. This was accomplished by a bulging of the soft palate to contact the posterior pharyngeal wall several centimeters cranial to the marker.

In one of the pigs, which also had a mandibular implant from a previous study, we were able to digitize the movements of the hyoid and mandible. During chewing and sucking, the hyoid and the epiglottis moved anteroposteriorly in synchrony. This parallelism was lost during swallowing (Fig. 5). As the epiglottis began its *descent, the hyoid ascended* towards the *mandible*. When the epiglottis reached its downmost position the hyoid was at or near its most elevated position.

Timing

Because preliminary analysis revealed minor but statistically significant individual differences in duration of swallowing, and because some animals did not eat all the food types, the statistical analysis was conducted using only individuals (pig #3, ferret #2) for which all data were available.

For solid foods the time interval between swallows was considerably longer than for successive liquid swallows (7-9 secs vs. 0.6-0.7 sec) (Table 1). This is a reflection of the fact that solids need to be chewed prior to being formed into a bolus.

The time duration of swallows as measured by epiglottic downturning and ascent, was remarkably similar for various foods in both the pig and ferret (Table 1). For both species the average total time for a swallow varied between 0.28 and 0.40 seconds. The total time taken for the epiglottis to move through one swallowing cycle was less for liquids than for hard chow in both the pig and the ferret ($p< 0.01$).

Even in the context of the swallowing duration, the downturning of the epiglottis was rapid (Table 2). Once again the two species were similar, with downturning lasting 0.07 sec (ferret) to 0.10 sec (pig) for liquids and 0.12 sec (pig) to 0.15 sec (ferret) for hard solids. The ferret liquid - solid difference was significant at $p <0.001$.

Once at the inferior point of its movement, the epiglottis did not ascend immediately but remained depressed until the bolus had completely passed its downturned tip. The epiglottis was in its downturned position more briefly for ferrets (0.07 - 0.09 seconds for liquids and solids respectively) than for pigs (0.13 - 0.17 seconds) (Table 1). The species difference was significant at $p<0.001$, and the tendency of the epiglottis to remain downturned longer for hard chow than for liquids for both the pig and ferret was also statistically significant at the 0.01 level.

The ascent from the downward position to a fully upright position averaged 0.06 - 0.05 secs in the pig and 0.13 - 0.16 seconds in the ferret (Table 2). Food type did not affect the ascent but the species difference was significant ($p < 0.001$).

In summary, the species differed in that pigs showed a longer downturned period and faster ascent than ferrets. The prolongation of swallowing duration for hard chow versus liquids in ferrets was mainly due to the slower descent of the epiglottis.

Bolus

Since epiglottic movement and bolus transit through the laryngopharynx were coordinated, the total swallow time of 0.3 - 0.5 sec was approximately the same time that it took a bolus of material to move from the oropharynx to the superior end of the esophagus.

The barium studies in the pig showed the bolus, whether solid or liquid, moving past the tip of the downturned epiglottis and into the esophagus. The epiglottis covered the laryngeal opening at the moment when the bolus moved past and thus certainly served to deflect the bolus away from the orifice. Although the completeness of the epiglottic seal was not determined directly, no food was seen entering the laryngeal orifice.

"Streaming" of material past an upright epiglottis that was locking the soft palate into place was not seen. However, immediately (within 0.2 sec.) in advance of a swallow, and observed with liquids only, there was occasionally a small spurt of material past the upright epiglottis (Fig. 7).

DISCUSSION

This study confirmed that the epiglottis of the pig lies on the posterior surface of the soft palate at rest and during chewing. In the ferret the normal position of the epiglottis was in close proximity to the anterior surface of the soft palate. These are the relationships expected for ungulates and carnivores, respectively (Negus, 1949). Contrary to Negus' predictions, however, the study showed clearly that the epiglottis always turns down over the laryngeal inlet during swallowing. The divergent anatomy of the two species had no effect on the commonalty of this behavior, nor did the solid or liquid nature of the bolus. We conclude that epiglottic downturning is probably a universal feature of mammalian swallowing.

Bolus formation during swallowing was also a constant phenomenon. Liquids, soft foods and solids were all formed into boluses at the posterior portion of the tongue superior to the laryngeal opening prior to being swallowed. "Streaming" of food was not noted except immediately prior to the beginning of a swallow and then only with liquids. This was probably due to the muscular contractions beginning the actual swallow and compressing the bolus material. These small spurts of material past the epiglottis could not have represented an alternative swallowing pathway because they were never seen except in conjunction with a normal swallow.

The fact that the hyoid and epiglottis moved in opposite directions during swallowing indicates that laryngeal closure is not a simple raising of the larynx but a true inversion of the epiglottis. Further confirmation was supplied by the changing angulation of the linear profile of the epiglottic marker.

The small amount of elevation of the tip of the soft palate was unexpected. The terminus of the soft palate seemed to track the movement of the bolus, while closure of the nasopharyngeal airway occurred more cranially. This situation is analogous to that described in man, where closure is effected in large part by the levator veli palatini muscles, which insert well cranial to the free edge of the soft palate (DuBrul, 1976).

Many authors have speculated that pressure from the bolus causes epiglottic movement (reviewed by Fink and Demarest, 1978). Our finding of almost simultaneous movement of both bolus and epiglottis is superficially consistent with the argument that bolus pressure induces movement of the epiglottis. On the other hand, the epiglottis stayed in the downward position until very little, if any, of the bolus remained on its superior surface. If it were simply bolus pressure that maintained the epiglottis in its depressed position, then the epiglottis should begin ascending earlier. In addition, it has been shown that epiglottic folding occurs in the absence of a bolus (Fink and Demarest, 1978). Another argument against the primacy of bolus pressure is the fact that liquids were actually swallowed faster than solids. The rapidity of epiglottic depression for liquids suggests that a large cohesive bolus is not a prerequisite. In any case the rapid descent of the epiglottis during liquid swallows contradicts the contention that this process can occur around an upright epiglottis.

These observations indicate that an additional mechanism is needed to account for the full range of epiglottic downturning. Fink and Demarest (1978) have theorized that in humans differential pressure on the epiglottic cartilage produced by the adjacent structures can fold the upright epiglottis into a downturned conoid-surfaced structure. Analogously, in other mammals the upward movement of the entire larynx may cause forceful contact between the upright epiglottis and other structures, initiating the downturning which then continues by virtue of the intrinsic bending properties of the epiglottic cartilage itself.

Ardran and Kemp (1952) calculated the speed of movement of the human epiglottis to be 1 cm/20 msec or 0.50 m/sec. In the pig the epiglottic marker descends through an arc of approximately 90 degrees. In a pig weighing 25 kg the epiglottis is approximately 30 mm long. This movement therefore represents a linear distance of 50 mm, resulting in a linear velocity of approximately 0.25 m/sec or 8 radians/sec expressed angularly. This is of the same order of magnitude as Ardran and Kemp's figure.

Having established that downturning of the epiglottis occurs, it must be asked if the epiglottis plays a role in glottal protection during swallowing. During swallowing the epiglottis is arched over the laryngeal entrance and serves to deflect the bolus away from the glottal opening and towards the esophagus. We did not directly investigate the tightness of the seal formed by the epiglottis. However, an epiglottis folded over the laryngeal opening would prevent any reasonable intake of air and could therefore be a physical cause of the apnea reported by others (Koening et al. 1990;

McFarland and Lund, 1993). It is also interesting to note that the duration of an epiglottic cycle for swallowing was 0.3 - 0.5 sec in both species. This compares favorably with the 0.5 sec of airway closure given by Koening et al. (1990) for human infants.

If there is an adaptation for maintaining breathing while eating in mammals as Negus, Laitman and others have hypothesized, it seems to be in the rapidity of the swallowing motion rather than in the ability of the epiglottis to maintain a patent airway by locking onto the soft palate while swallowing. Inhalation and olfactory monitoring of the environment must stop during the 0.5 sec required for epiglottic depression. The disadvantage would be greater during drinking than during mastication because swallowing takes up approximately 50% of drinking time. What are the implications for survivability? Interestingly, many animals appear to be particularly vigilant while drinking. Also, if the intra-narial epiglottis is a modification that optimizes olfaction as Negus has stated, then is man truly at an olfactory disadvantage for not having this anatomical relationship? Since man is able to breathe through the nose at will by maintaining lip competence, the inability of the epiglottis to seal off the oral cavity during respiration is no disadvantage. The relatively dull sense of olfaction found in man is probably not due to the pathway of inspired air at all but to the differences in neurosensory apparatus when compared to animals with a keener sense of smell.

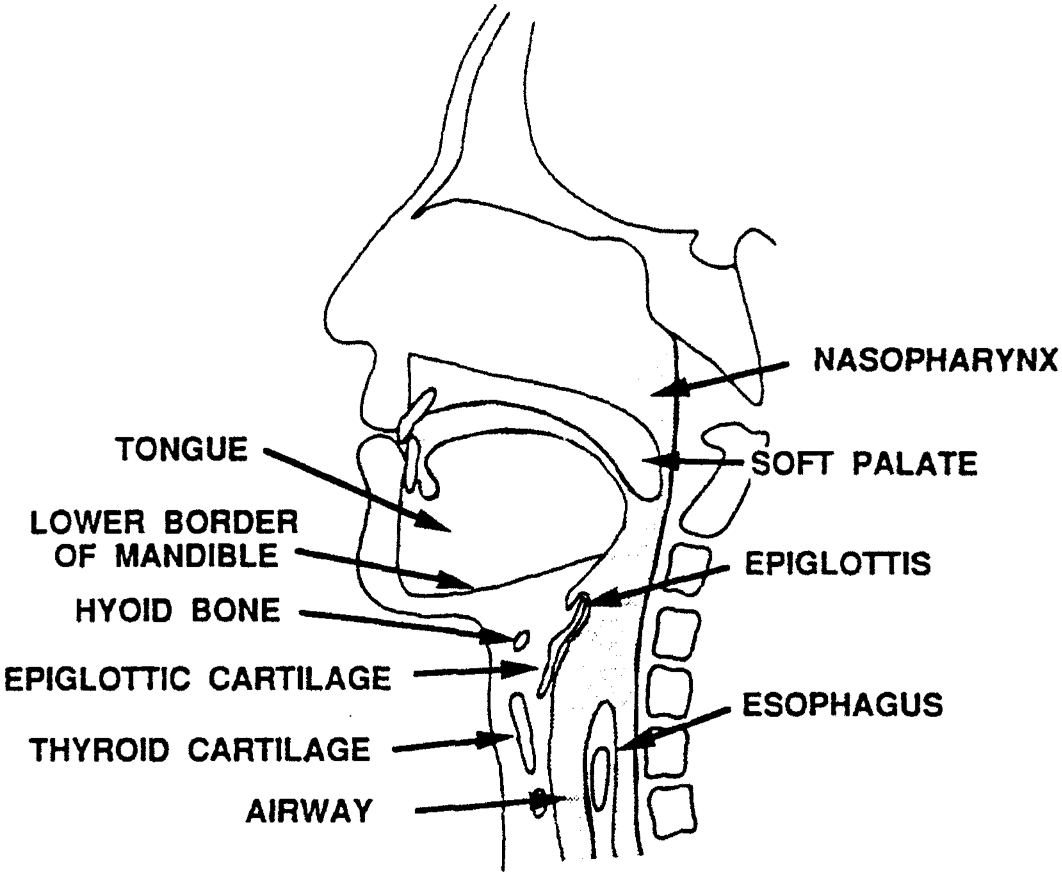


Fig. 1A Adult human at rest
(adapted fr. Cleall, 1965)

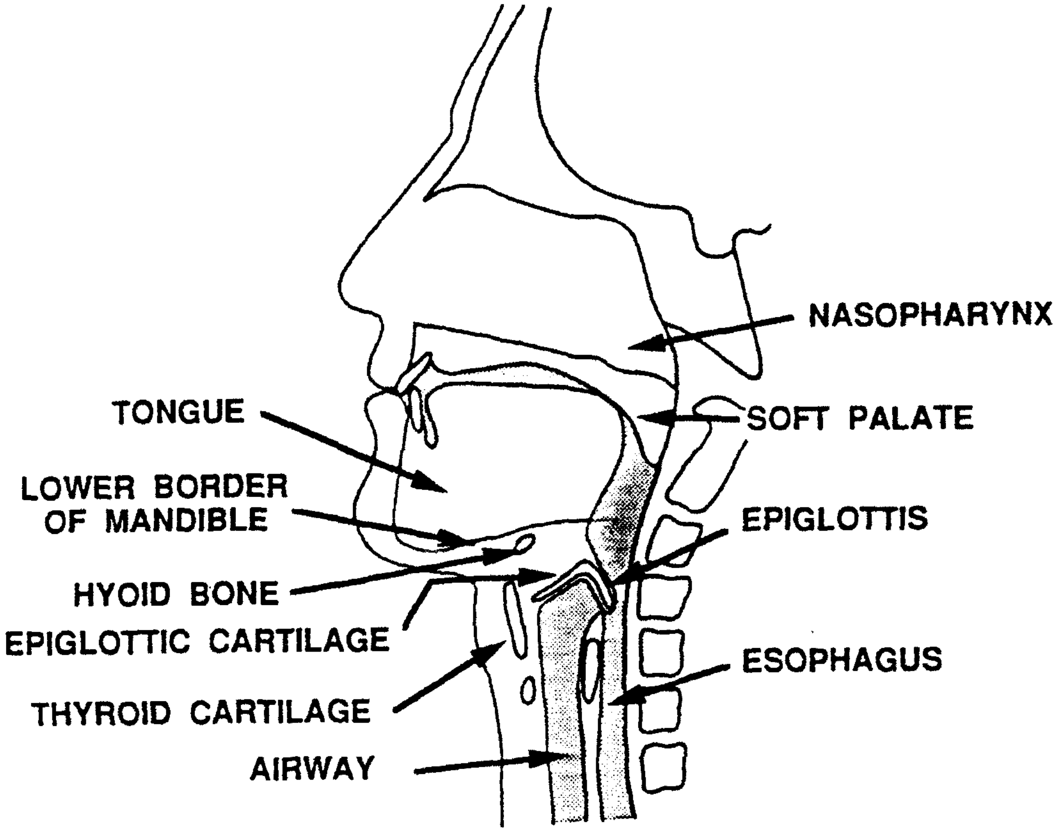


Fig. 1B **Adult human swallowing**
(adapted fr. Cleall, 1965; DuBrul, 1976; Ekberg, 1983)

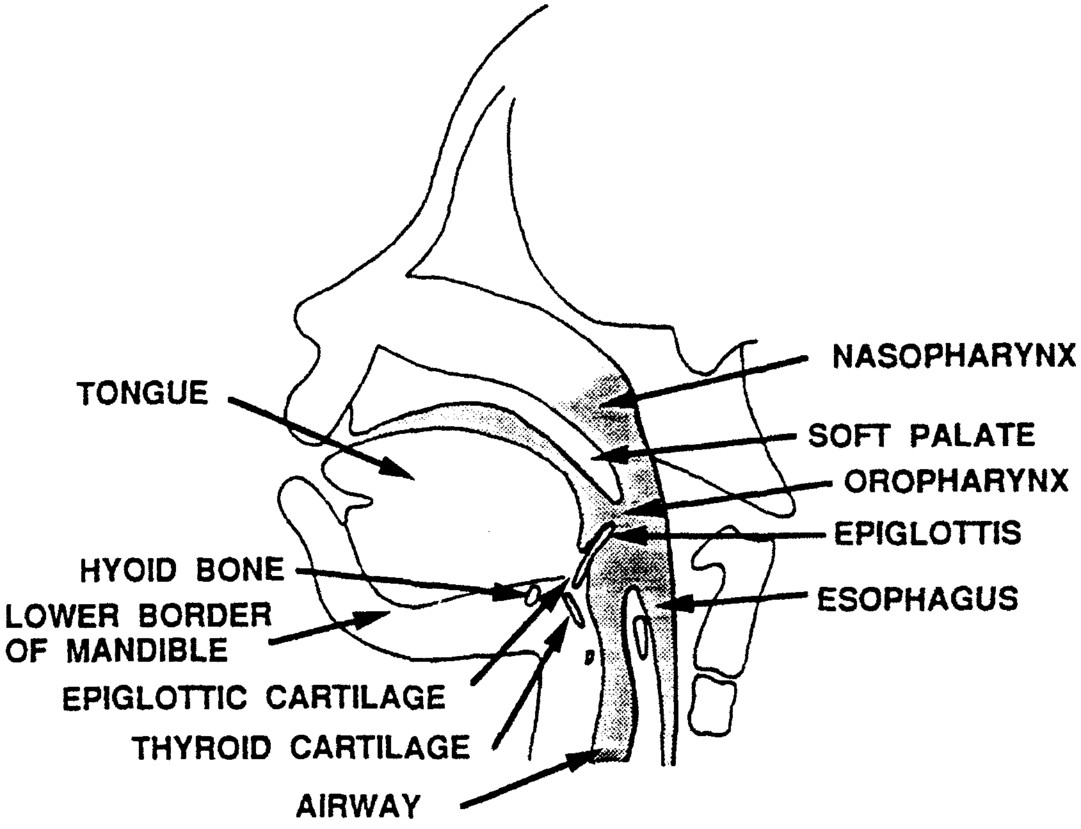


Fig.1C Human infant at rest
(adapted fr. Bosma, 1986)

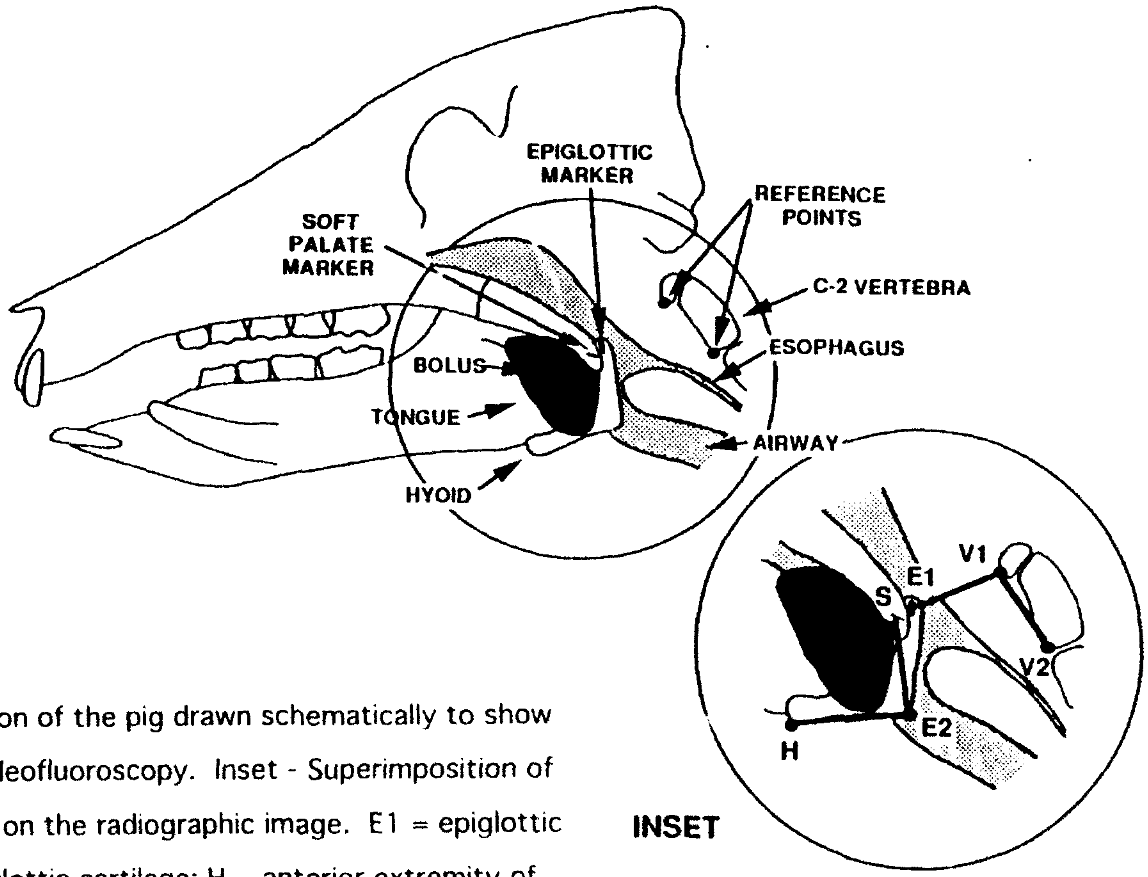


Fig. 2 Sagittal section of the pig drawn schematically to show structures seen during videofluoroscopy. Inset - Superimposition of computer digitized figure on the radiographic image. E1 = epiglottic marker; E2 = base of epiglottic cartilage; H = anterior extremity of hyoid bone; S = soft palate marker; V1, V2 = vertebral points used as *references*

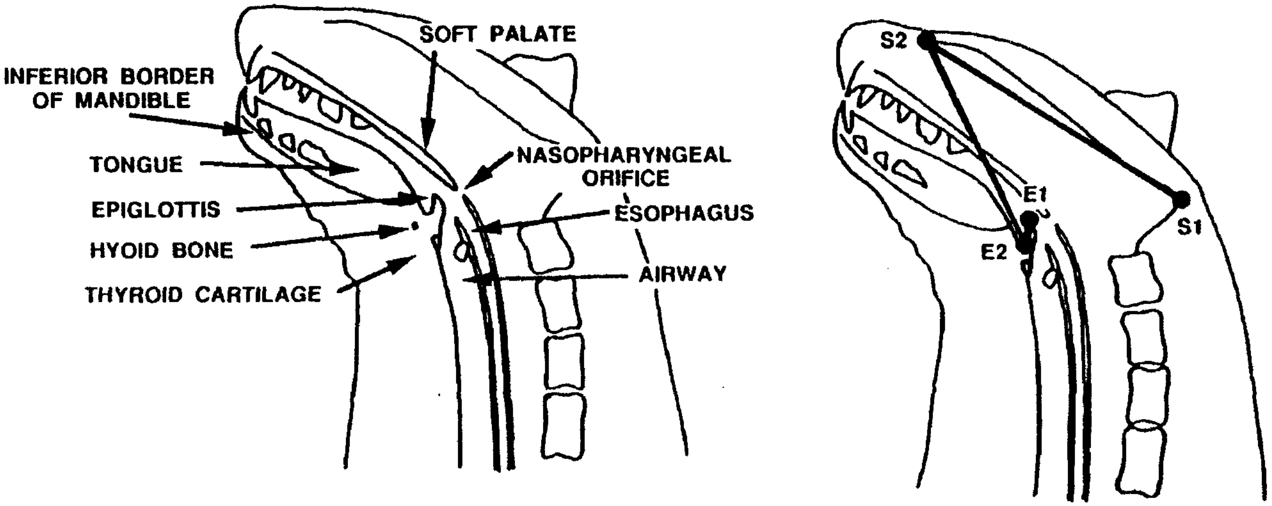
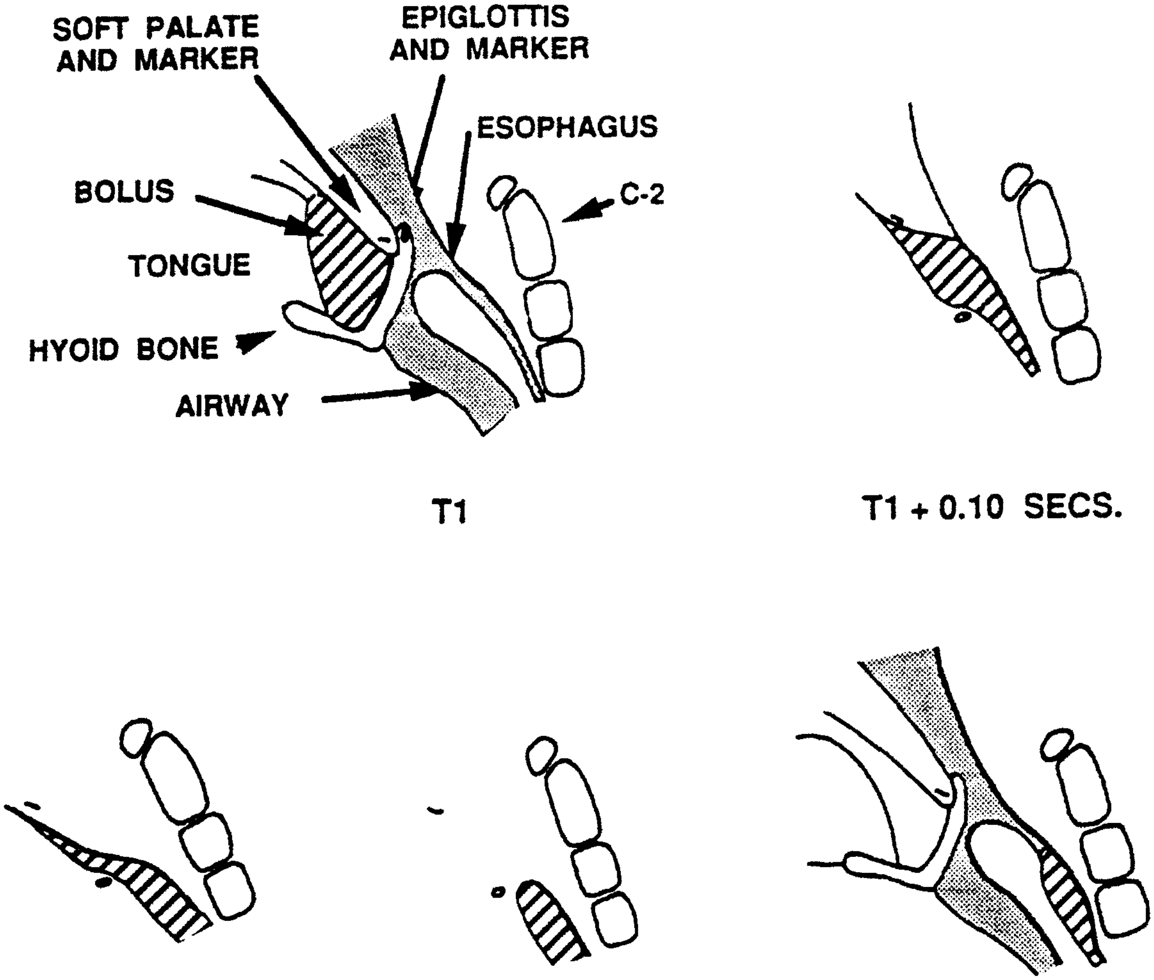


Fig. 3 *Sagittal section of the ferret.* Inset - *Superimposition* of computer digitized figure. E1 = distal end of epiglottic marker; E2 = proximal end of epiglottic marker; S1 and S2 = reference skull points.



T1

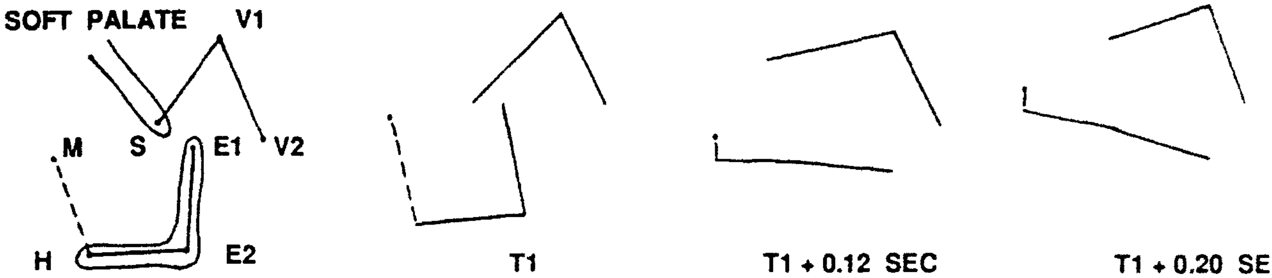
T1 + 0.10 SECS.

T1 + 0.15 SECS.

T1 + 0.23 SECS.

T1 + 0.29 SECS.

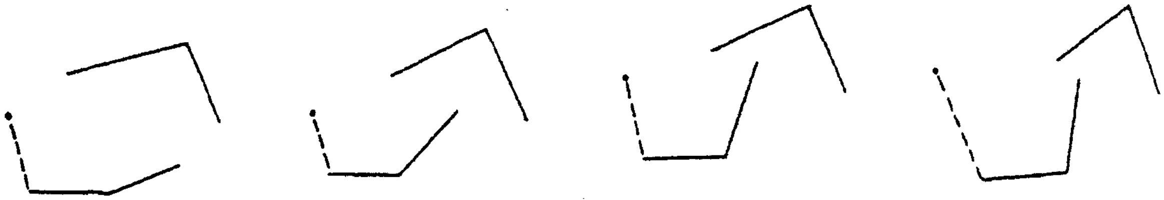
Fig. 4 Sketches of selected frames from a pig (#3) swallowing liquid mixed with barium. Conventions and abbreviations as in Figure 2. T1: Immediately prior to initiation of the swallow, a bolus has formed in the space bounded by the tongue, soft palate and epiglottis. T1 + 0.10 secs: Beginning of swallow. The bolus is flowing past the downturned epiglottic marker. T1 + 0.15 secs: The bolus continues flowing past the downturned marker. T1 + 0.23 secs: The bolus has passed the larynx, and the epiglottic marker begins to ascend. T1 + 0.29 secs: With the epiglottis in the upright position, the swallow is complete.



T1
ALL STRUCTURES
IN IMMEDIATE
PRE-SWALLOW
POSITION

T1 + 0.12 SEC
SOFT PALATE ASCENDS
EPIGLOTTIS DESCENDS
HYOID ASCENDS

T1 + 0.20 SEC
EPIGLOTTIS
DOWNTURNED



T1 + 0.30 SEC
EPIGLOTTIS ASCENDING
HYOID DESCENDING

T1 + 0.32 SEC
EPIGLOTTIS ASCENDING
SOFT PALATE
DESCENDING

T1 + 0.34 SEC
EPIGLOTTIS
ASCENDING

T1 + 0.36 SEC
ORIGINAL POSITIONS
RESTORED

Fig. 5 Digitized frames of pig (#2) swallowing hard chow. Conventions as in Figure 2. This pig had an easily visible hyoid bone and a mandibular implant, which were digitized in addition to the markers and reference points. The soft palate is raised between T1 and T1 + 0.12 sec and remains elevated until T1 + 0.32 sec. The hyoid is elevated and the epiglottis depressed simultaneously with palatal elevation. H = hyoid bone; other abbreviations as in Figure 2.

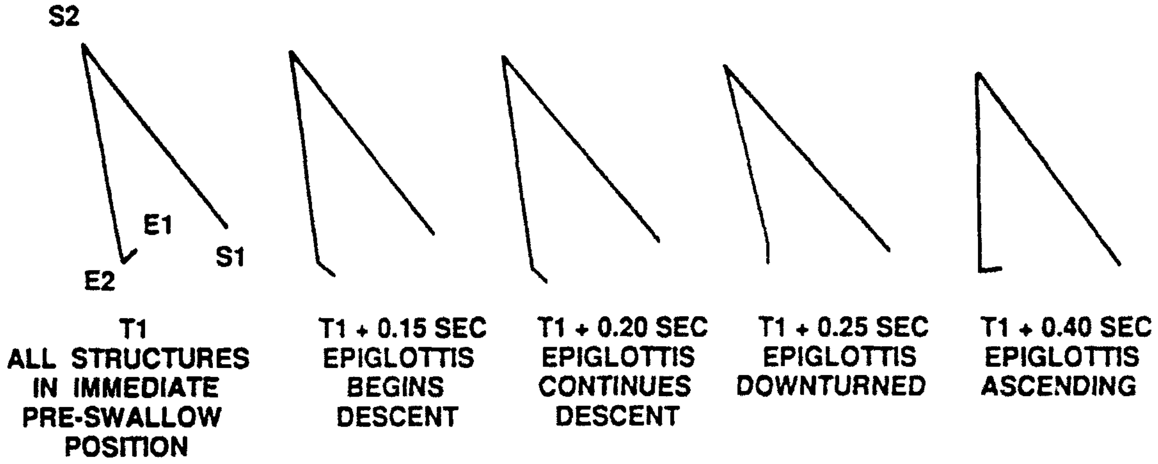


Fig. 6 Series of digitized frames of ferret (#2) swallowing hard chow. T1: The epiglottis is upright, just prior to the swallow. T1 + 0.15 secs: The swallow begins with downturning of the epiglottis. T1 + 0.20 secs: The epiglottis continues in the downturned position. T1 + 0.25 secs: The epiglottis reaches maximum depression. T1 + 0.40 secs: The epiglottis has returned to normal upright position, completing the swallow. Abbreviations as in Figure 3.

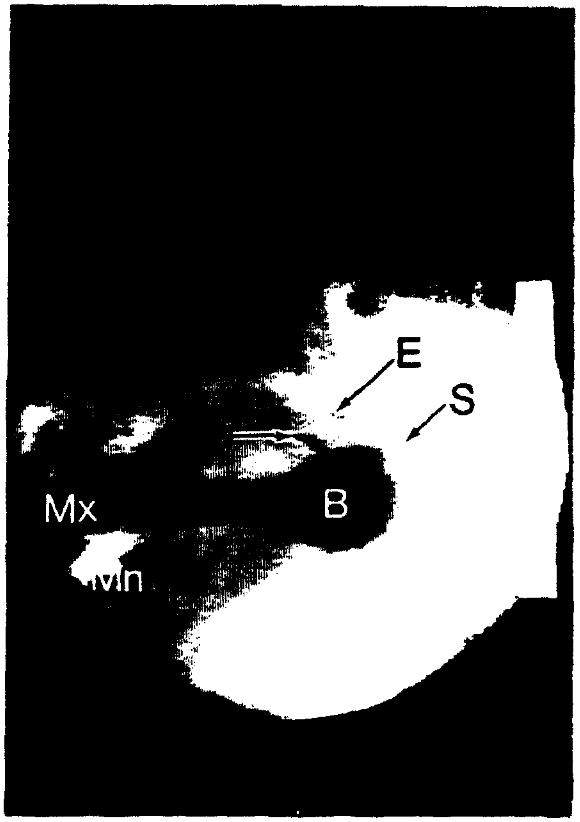

E
S
Mx
B
Mn

Table 1 Duration and Frequency of Swallows For the Pig and Ferret for Various Types of Food

		Time Duration of Swallow [Mean (secs) ± S.D., N]	Time Between Swallows [Mean,(secs) ± S.D., N]
PIG	Liquid	0.31 ± 0.03, 33	0.62 ± 0.13, 33
	Soft chow	0.34 ± 0.09, 59	8.88 ± 3.91, 36
	Hard chow	0.36*± 0.02, 7	N/A
FERRET	Liquids	0.28 ± 0.08, 31	0.68 ± 0.39, 31
	Hard chow	0.40*± 0.10, 13	7.44 ± 2.99, 46

*significantly different from liquid at $p<0.01$

Table 2 Time Intervals for Epiglottic Movement

Descent time (D), Time spent in descended position (T), Ascent time (A)

		Pig [Mean (secs) ± S.D., N]	Ferret [Mean (secs) ± S.D., N]
Liquid	D	0.10 ± 0.03, 23	0.07 ± 0.02, 31
	T	0.13 ± 0.05, 23	0.07 ± 0.02, 31
	A	0.06 + 0.03, 23	0.13 + 0.03, 31
Soft Chow	D	0.08 ± 0.02, 21	-------
	T	0.15 ± 0.03, 21	-------
	A	0.07 + 0.01, 21	-------
Hard Chow	D	0.12 ± 0.03, 7	0.15 ± 0.04, 14
	T	0.19 ± 0.02, 7	0.09 ± 0.01, 13
	A	0.05 + 0.02, 7	0.16 + 0.05, 13

BIBLIOGRAPHY

Ardran, G.M. and F.H. Kemp (1955) A radiographic study of movements of the tongue in swallowing. Dental Practitioner. 5:252-262.

Ardran, G.M. and F.H. Kemp (1952) The protection of the laryngeal airway during swallowing. British Journal of Radiology. 25:406-416.

Barclay, A.E. (1933) The Digestive Tract. Cambridge: The University Press.

Biewener, A.A., G.W. Soghikian and A.W.Crompton (1985) Regulation of respiratory airflow during panting and feeding in the dog. Respiration Physiology. 61:185-195.

Bickerton, D. (1990) Language and Species. Chicago: The University of Chicago Press.

Bosma, J.F. (1986) Anatomy of the Human Head. Baltimore: The Johns Hopkins University Press.

Cleall, J.F. (1965) Deglutition: a study of form and function. Am. J. Orthodontics. 51:566-594.

Crelin, E.S. (1973) Functional Anatomy of the Newborn. New Haven: Yale University Press.

Crelin, E.S. (1987) The Human Vocal Tract. New York: Vantage Press.

DuBrul, E.L. (1976) Biomechanics of speech sounds. Annals of the New York Academy of Sciences. 280:631-642.

Ekberg, O. (1983) Epiglottic dysfunction during deglutition in patients with dysphagia. Arch. Otolaryngol. 109:376-380.

Ekberg, O. and S.V. Sigurjonsson (1982) Movement of the epiglottis during deglutition. Gastrointest. Radiol. 7:101-107.

Fink, B.R. and R.J. Demarest (1978) Laryngeal Biomechanics. Cambridge, Massachusetts: Harvard University Press.

Hamilton, W.J., ed. (1976) Textbook of Human Anatomy, Second Edition. Saint Louis, Missouri: The C.V. Mosby Company.

Herring, S.W. and R.P. Scapino (1973) Physiology of feeding in miniature pigs. J. Morph. 141:427-460.

Johnstone, A.S. (1942) A radiological study of deglutition. Journal of Anatomy. 77:97-100.

Kenny, D.J., M.J. Casas and K.A. McPherson (1989) Correlation of ultrasound imaging of oral swallow with ventilatory alterations in cerebral palsied and normal children : Preliminary observations. Dysphagia. 4:112-117.

Koenig, J.S., A.M. Davies and B.T. Thach (1990) Coordination of breathing, sucking, and swallowing during bottle feedings in human infants. J. Appl. Physiol. 69:1623-1629.

Laitman, J.T., E.S. Crelin and G.J. Conlogue (1977) The function of the epiglottis in monkey and man. The Yale Journal of Biology and Medicine. 50:43-48.

Laitman, J.T. and E.S. Crelin (1980) Developmental change in the upper respiratory system of human infants. Perinatology-Neonatology. 4:15-22.

Laitman, J.T. and R.C. Heimbuch (1982) The basicranium of pre-pleistocene hominids as an indicator of their upper respiratory systems. Am. J. of Phys. Anthrop. 59:323-343.

Lieberman, P., E.S. Crelin and D.H. Klatt (1972) Phonetic ability and related anatomy of the new born and adult human, Neanderthal man, and the chimpanzee. Am. Anthropol. 74:287-307.

McFarland, D.H. and J.P. Lund (1993) An investigation of the coupling between respiration, mastication, and swallowing in the awake rabbit. Journal of Neurophysiology. 69:95-108.

Magriples, U. and J.T. Laitman (1987) Developmental change in the position of the fetal human larynx. Am. J. of Phys. Anthrop. 72:463-472.

Mosher, H. P. (1927) X-ray study of movements of the tongue, epiglottis, and hyoid bone in swallowing, followed by a discussion of difficulty in swallowing caused by retropharyngeal diverticulum, post-cricoid webs and exostoses of cervical vertebrae. The Laryngoscope. 37:235-262.

Negus, V.E. (1949) The Comparative Anatomy and Physiology of the Larynx. London: William Heinemann Medical Books Ltd.

Ramsey, G.H., J.S. Watson, R. Gramiak and S.A.Weinberg (1955) Cinefluorographic analysis of the mechanism of swallowing. Radiology. 64:498-518.

Ross, P.E. (1991) Hard words. Sci. Am. 264:138-147.

Rushmer, R.F. and J.A. Hendron (1951) The act of deglutition: A cinefluorographic study. J. Appl. Physiology 3:622-630.

Sasaki, C.T., P.A. Levine, J.T. Laitman, E.S. Crelin (1977) Postnatal descent of the epiglottis in man. Arch. Otolaryngol. 103:169-171.

Saunders, J.B., C. Davis, E.R. Miller (1951) *The mechanism of* deglutition (second stage) as revealed by cine-radiography. Annals of Otology, Rhinology, and Laryngology. 60:897-916.

Selley, W.G., R.E. Ellis, F.C. Flack and W.A. Brooks (1990) Coordination of sucking, swallowing and breathing in the newborn: Its relationship to infant feeding and normal development. British J. of Disorders of Communication. 25:311-327.

Shaker, R., W.J. Dodds, R.O. Dantas, W.J. Hogan and R.C. Arndorfer (1990) Coordination of deglutitive glottic closure with oropharyngeal swallowing. Gastroenterology. 98:478-1484.

Siegel, S. and N. J. Castellan (1988) Nonparametric Statistics For the Behavioral Sciences. New York: McGraw Hill.

Sisson, S. and J.D. Grossman (1938) The Anatomy of the Domestic Animals. Philadelphia: W.B. Saunders.

Welin, S. (1939) Deglutition anomaly simulating hypopharyngeal cancer. Acta Radiologica. 20:452.