Mechanism of Intraoral Transport in Macaques

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ABSTRACT All mammals have the same divisions of cyclic movement of tongue and hyoid during mastication: a protraction or forward phase that begins at minimum gape, and a retraction or return phase. Nonanthropoid mammals transport food from the oral cavity to the oropharynx during the return phase; food on the dorsal surface of the tongue moves distally while the tongue is retracted. Macaques, however, transport food during the protraction phase of tongue/hyoid movement. Food is squeezed posteriorly by contact between the tongue surface and the palate anterior to the food.

This mechanism of transport is occasionally seen in nonanthropoid mammals when they are transporting liquids from the oral cavity to the oropharynx. It has, however, not been seen when these mammals transport solid food. One morphological basis for this difference is the reduction in height of the rugae of the palate of macaques. In most mammals these rugae are pronounced ridges that are able to hold food in place during protraction as the tongue slides forward beneath the food.

Anthropoids and other mammals differ in the way they store food prior to swallowing. When macaques transport food to the oropharynx, usually they swallow in the next cycle, but always in the next 2 or 3 cycles. Most mammals transport and store food in the oropharynx for several cycles before a swallow clears that region of food. This behavior is correlated with differences in morphology of the oropharynx; anthropoids have reduced valleculae, the area in which other mammals store food prior to swallowing.

The mechanisms used by certain mammals for intraoral food transport are well known. Crompton and Weijs-Boot (in prep.) have shown the relationship between the relevant anatomical structures and their role in transport in the opossum. Franks and German (in prep.) document the movements of tongue and hyoid in hyrax food transport, and demonstrate the significance of the biphasic nature of their movement cycle. During the protraction phase, markers in the tongue move forward relative to the hard palate, and the hyoid moves up and forward at the same time in hyraxes and other nonanthropoids. Food in the oral cavity is held stationary because it is in contact with the pronounced ridges of the palatal mucosa. The tongue dorsum slides forward beneath the relatively stationary food so that the more posterior regions of its surface are brought into contact with the food. This protraction phase begins at the start of jaw-opening and continues almost until the end of the jaw-open phase.

In the second phase of the cycle in nonanthropoids, the return phase, the tongue moves backward. Contact between food and the palatal ridges is broken so that as the tongue moves back in the oral cavity, food on its surface is moved toward the oropharynx. In *Procavia capensis* (Franks and German, in prep.), *Didelphis marsupialis* (Crompton and Weijs-Boot, in prep.), *Felis catus* (Hiiemae et

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al., 1979), and *Lemur fulvus* (Franks, unpublished data), throughout most of the masticatory sequence processed food collects in the vallecular region of the oropharynx. The valleculae are a pair of pouches at the back of the oropharynx in front of or on either side of the epiglottis. In cycles containing a swallow the bolus is moved out of the valleculae, past the lifted soft palate, around the epiglottis, and into the esophagus.

A different mechanism is sometimes seen during lapping in the opossum (Crompton and Weijs-Boot, in prep.) and the cat (Hiiemae, 1978; Thexton, pers. comm.). In such transport cycles, liquid is collected in a depression on the tongue surface. The surface of the tongue anterior to the liquid is elevated to contact with the palate, squeezing the liquid in a posterior direction. The surface of the tongue posterior to the liquid is lowered so that the liquid flows distally.

This study examines the mechanisms of intraoral transport used by *Macaca fasicularis*, the "crab-eating macaque," in feeding on apple. The comparison of macaques with other mammals includes a discussion of the differences in oral anatomy and how these differences relate to intraoral transport.

METHODS

This study of food transport and swallowing in macaques is part of a larger investigation examining several aspects of masticatory function in these anthropoid primates. Two adult females and one adult male macaque (*Macaca fascicularis*) were sedated and anesthetized with a mixture of Ketamine and Ace Promazine. Two sterilized metal markers were inserted into the body of the tongue with a hypodermic syringe, one in the middle third and one in the posterior third along an anterior-posterior axis. These markers are essential for tracing the movement of regions of the tongue. A small metal marker was attached to the hyoid with surgical sutures in the anesthetized animal. After recovery the animals were filmed sitting in a Plexiglas restraining chair while eating apples, monkey chow, carrot, bananas, or oranges. This paper is based on results for experiments done with apple, but the results do not vary significantly with the different kinds of food. Movement was recorded in lateral projection using 16mm Kodax plus-X reversal film at 100 fps with a Siemens cineradiographic apparatus and an Eclair GV16 high speed cine-camera. In some films the apple was coated or injected with barium to make it radiopaque.

The method of film analysis was identical to previous mammalian experiments (Hiiemae and Crompton, 1984). In the film it is easy to distinguish the markers, the amalgams, the food, and the dorsal, or upper, surface of the tongue. A Vanguard Motion Analyzer was used for frame-by-frame analysis. Approximately 100 cycles were analyzed. The chew cycle with transport and the subsequent swallow, which are described in this paper, are typical of the data that were obtained for these three animals. Acetate overlay tracings of individual frames were used to obtain a detailed description of some aspects of food transport.

RESULTS

Anatomy and overview of food transport

Anthropoids, as is true of other mammals, usually ingest food and then move it from the oral cavity through the oropharynx to the esophagus. In mammals with long oral cavities, Stage I transport is the process that moves food from the front of the mouth to the region of the cheek teeth. In mammals with long oral cavities, such as hyraxes and opossums, this process is a more significant portion of transport than in macaques, where food can be ingested directly to the region of the cheek teeth. Stage II transport is the movement of food from the region of cheek teeth into the oropharynx, the space that is behind the junction between the soft and hard palates, above the posterior tongue surface, and below the soft palate. This area is equivalent to what Hiiemae and Crompton (1984) refer to as the anterior compartment of the oropharynx. Anthropoids lack the large vallecular regions, pouches continuous with the back of the oropharynx, of other mammals and, hence, do not form a bolus in the oropharynx prior to swallowing. If a small amount of food is ingested, it may be carried on the tongue for a cycle prior to swallowing. During a swallow, the soft palate lifts and the epiglottis folds back (Getty, 1975) to prevent food from entering the nasopharynx and the trachea.

Three major components of the masticatory apparatus, the tongue, the hyoid complex which forms the base of the tongue, and the jaws, contribute to the mechanism of food transport. Each of these structures shows biphasic cyclic behavior. The movement of the jaws, usually measured by change in gape, can be most easily divided into opening and closing phases. The body of the tongue and the hyoid, as reflected by change in position of the implanted markers, show a forward phase and a return phase. As the jaw reaches minimum gape, i.e., the beginning of the opening phase, the tongue and hyoid markers begin to move upward and forward. When food is about to be transported, the middle tongue marker also begins an upward and anterior phase of movement. This phase is the same as the tongue/hyoid protraction phase described for hyraxes (Franks and German, in prep.) and the other mammals observed to date (Hiiemae and Crompton, 1984). The tongue-return phase is not described in this paper, although typical patterns of movement are shown in Figures 2 and 4.

Mechanism of transport

When macaques are feeding on solid food, three kinds of cycles are seen: 1) chewing without transport, 2) chewing with transport, and 3) swallowing. Chewing without transport is manipulation of food, a processing procedure designed to reduce consistency to a point where the animal can swallow. Chewing with transport is the movement of processed food from the area of the cheek teeth to the oropharynx. In the two females, cycles that include transport of food to the oropharynx were usually followed by a swallow cycle in which food from the oropharynx moved into the esophagus. In the male, however, as many as three of these transport cycles occurred prior to a swallow. The data described here are for macaques eating apple, but the results hold for other kinds of food. Figure 1 shows tracings of significant events in a cycle with Stage II transport. Figure 2 shows jaw movement and orbits of movement for the hyoid, the middle, and the posterior tongue markers in the same cycle.

The cycle begins at the start of the tongue/hyoid protraction phase (frame 315). At this time the jaw is still closing, but it has almost achieved minimum gape. The dorsal surface

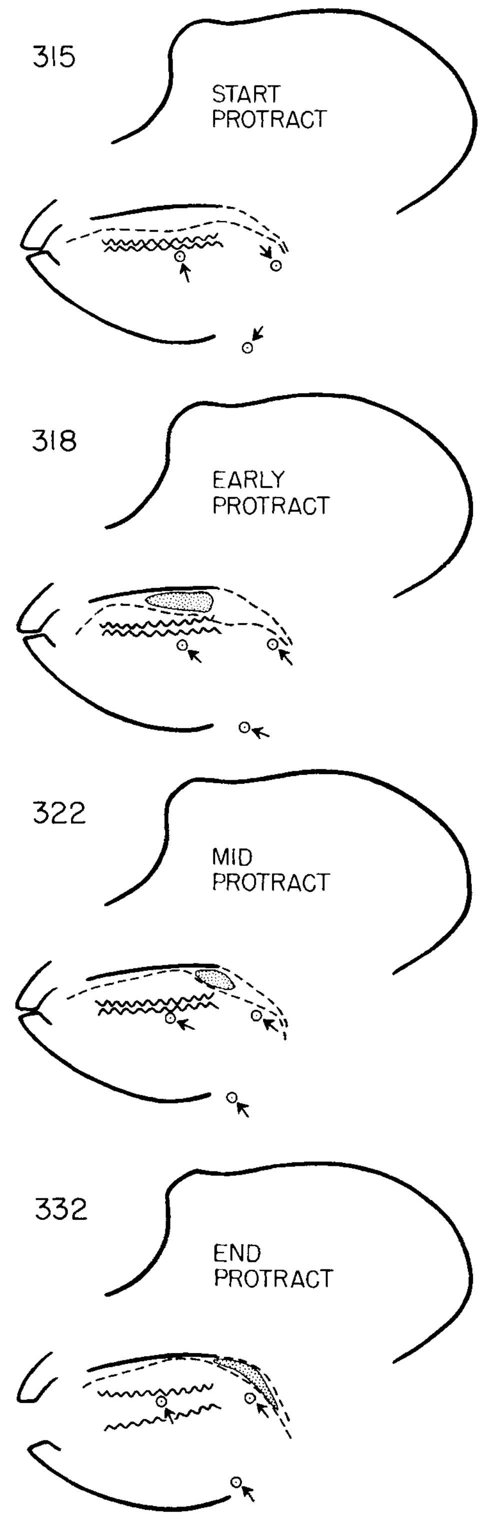

Fig. 1. A series of tracing from a cycle during which macaque number 1 is moving food from the oral cavity to the oropharynx. Food is represented by the shaded area. Marker position for the hyoid and two tongue markers are circles with a dot in the center. The arrows show movement of the marker in the interval between the illustrated frame and the frame immediately preceding it. The dorsum of the tongue and the soft palate are represented by dotted lines. The interval between successive frames lasts approximately 10 milliseconds.

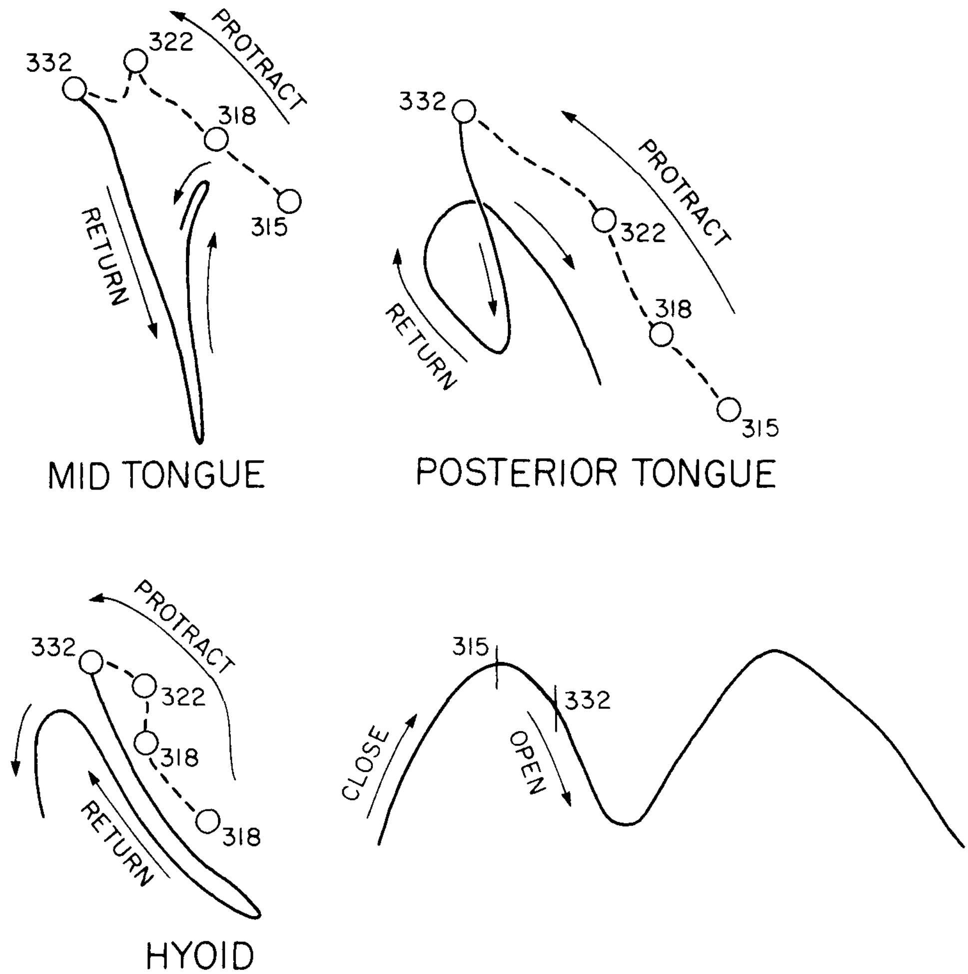

Fig. 2. Orbits of movement for the hyoid and two tongue markers for the Stage II transport cycle shown in Figure 1. During the protraction phase the hyoid and tongue markers move up and forward. During the return phase they exhibit a more complex series of movements. Frames illustrated in Figure 1 are circled and numbered in the orbits. Jaw movement for the cycle is shown in the lower panel of this figure.

of the tongue is approximately parallel with the hard palate. The posterior dorsal surface of the tongue is sloped downward, approximately parallel with the soft palate. Between the soft palate and the posterior tongue dorsum is the space into which food will be transported in this cycle. Between frames 315 and 318 the configuration of the tongue dorsum changes considerably. The tongue surface forms a long slope from front to back. The highest region is anterior to the middle tongue marker. In that area the tongue dorsum is in contact with the hard palate. The most ventral region of the tongue surface is in the area that forms the floor of the oropharynx.

The middle and posterior tongue markers have moved up and forward since the beginning of the cycle, as is seen in frame 318. Food that has been collected on the dorsal surface of the tongue lies just above the middle marker. Contact between the tongue and palate anterior to this collected food insures that the food will not move forward in the oral cavity. Posterior to the bolus the tongue slopes downward so that movement to the oropharynx is facilitated.

The mechanism by which food is moved from the oral cavity to the oropharynx of macaques is elucidated by comparing the reationship of the tongue surface and the hard palate in frames 318 and 322. The area of contact between these two structures has increased in the interval between these frames. Increased contact, which occurs anterior to food collected on the tongue dorsum, "squeezes" food toward the oropharynx. The tongue surface posterior to the food that is being moved in frame 332 is still sloped downward, as it was in frame 318, so that continued transport of food from the oral cavity is facilitated. In the interval between frames 318 and 322, the middle and posterior tongue markers and the hyoid have moved up and forward (Fig. 1). Food has been moved posteriorly in the oral cavity by the mechanism just described.

During the remainder of the tongue/hyoid protraction phase, both tongue markers and the hyoid continue to move up and forward. Frame 322, which is the end of the phase, shows that food has been moved into the oropharynx. Posterior transport of food was accomplished by increasing the area of contact between the tongue dorsum and the subpalatal mucosa.

Food transport in swallow cycles.

Figure 3 shows tracings of events that are important for the transport of food before and during a macaque swallow. Orbits of the hyoid and two tongue markers are shown in Figure 4. Frame 369 of Figure 3 occurs at the end of the cycle that precedes the swallow. At this time food has been collected on the tongue dorsum in the region of the cheek teeth. There is also food in the oropharynx. It was moved to that region in the cycle described in the preceding section.

Frame 371 in Figure 3 represents the start of the tongue/hyoid protraction phase in an anthropoid swallow cycle. The jaw is still closing, but minimum gape has almost been achieved. The tongue dorsum is in an arched configuration, with the highest region above the middle tongue marker. The lowest region is that part of the tongue that forms the floor of the oropharynx. Food lies along the dorsal surface from the middle region to the oropharynx. Contiguity has been established between food that is being moved from the oral cavity to the oropharynx in this cycle with food that was moved to that region in the previous chewing cycle. The soft palate has already been elevated so that it no longer contacts the posterior tongue dorsum. Despite the lack of contact between the tongue and soft palate, significant movement of food out of the oropharynx has not occurred. In frame 373 food collected on the tongue dorsum within the oral cavity is pushed through the fauces. This movement of food was accomplished by elevation of the tongue surface anterior to the food, so that food is "squeezed" toward the oropharynx by pressure between the tongue dorsum and the subpalatal mucosa. The mechanism of transport is the same as that seen in the previous chewing cycle (described above). Significant movement of food through the oropharynx into the pharynx has not yet occurred. The middle and posterior tongue markers have moved up and forward in the interval between frames 371 and 373; the hyoid has moved up.

Frame 377 shows the beginning of movement of food into the esophagus. The border between the esophagus and the pharynx is (presumably) the area of constriction of the bolus that is being swallowed. Continued dorsal movement of the tongue markers shows that food is still being "squeezed" in a posterior direction. The fact that significant movement of the leading edge of the bolus is occurring suggests that the pharyngeal constrictors are now active. In previously illustrated frames the leading edge of the bolus was relatively stationary despite the activity of the tongue. Final movement of food into the esophagus is, therefore, achieved by combined activity of the tongue and the pharyngeal constrictors. In the interval between frames 373 and 377 tongue markers have continued to move dorsally. A noticeable anterior component has been added to movement of the hyoid, which was moving in a predominantly upward direction in the previously discussed portion of the cycle.

In frame 382 the posterior dorsum of the tongue is seen to lie close to the ventral surface of the soft palate so that the space between these structures is to a large extent obliterated. This has been accomplished by movement of the tongue in a posterior direction, as indicated by the posterior tongue marker. The effect is to clear the oropharynx of food. The hyoid, during the same period, has moved forward.

The tracings and orbits in Figure 4 demonstrate that the period of posterior movement of the tongue, especially that region that lies below the soft palate, and of anterior movement of the hyoid, is the period when most (or all) of a bolus is moved out of the oropharynx and into the esophagus. This period of tongue/hyoid activity occurs only in swallow cycles. It is always correlated with movement of food out of the oropharynx and

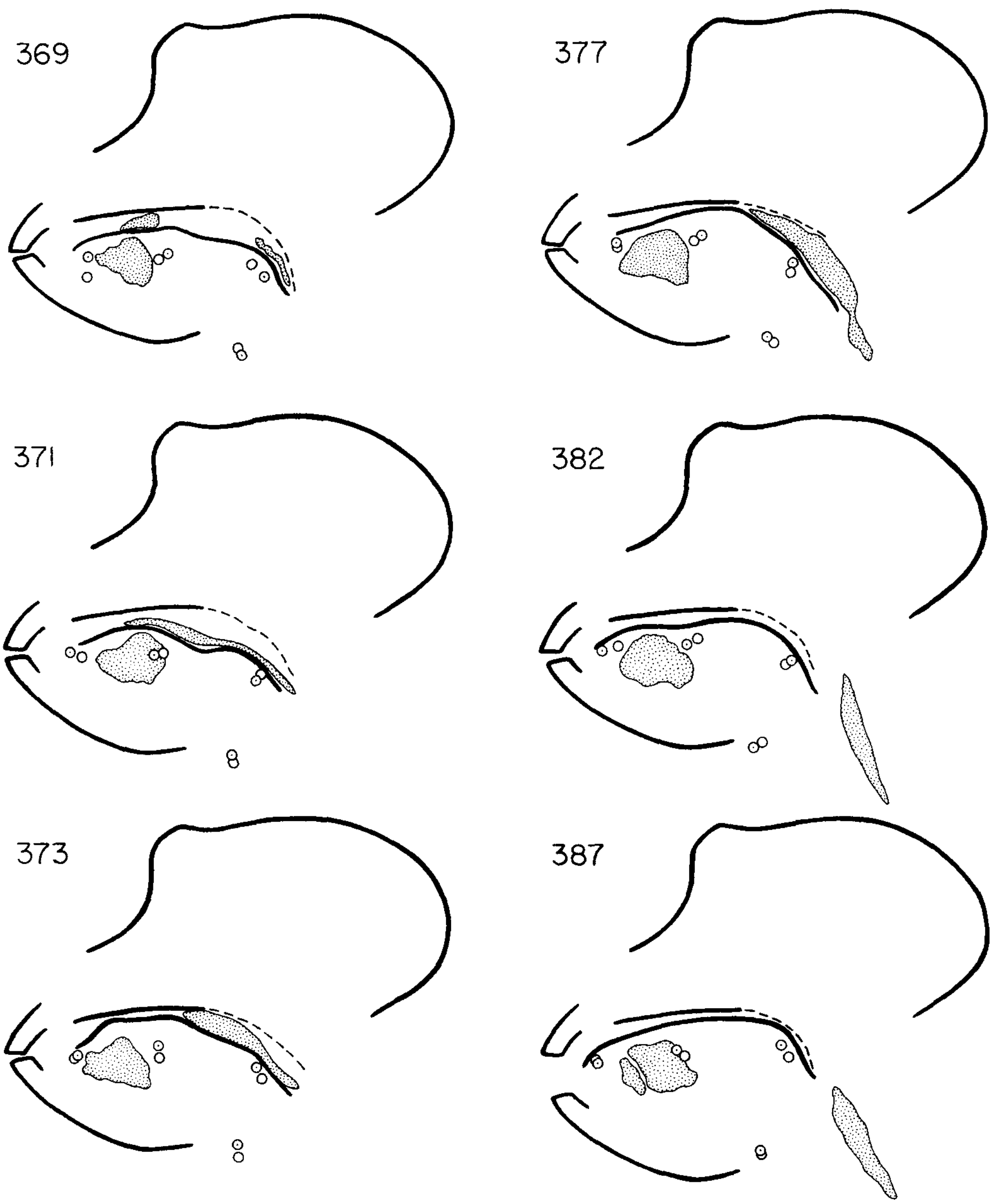

Fig. 3. A series of tracings for a cycle during which macque number 1 is swallowing. Present positions of tongue and hyoid markers are represented by circles with a dot in the center. Position of the markers in the previous frame are represented by open circles. Food is shown as a shaded area. The tongue dorsum and the hard palate are solid lines. The ventral surface of the soft palate is a dotted line.

into the esophagus. It always occurs in the middle of an otherwise "typical" protraction phase. Following this period of activity, tongue/hyoid protraction resumes.

DISCUSSION

Comparison of chew and swallow cycles.

The mechanism by which solid food is moved from the oral cavity to the oropharynx by macaques is the same for both chew cycles and swallow cycles. The posterior tongue dorsum is lowered. The middle/anterior region of the tongue dorsum is raised. Food that has been collected on the tongue surface lies behind the area that is elevated. Food is "squeezed" toward the oropharynx by progressive elevation of the region of the tongue

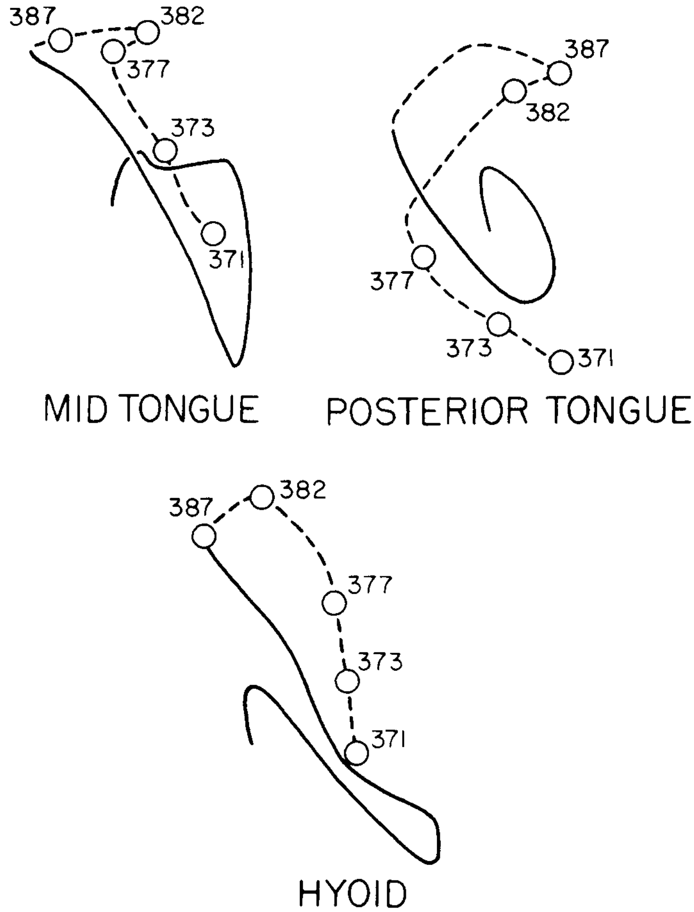

Fig. 4. The orbits of movement for two tongue markers and the hyoid for the swallow cycle illustrated in Figure 3. Frames illustrated in Figure 3 are circled and numbered in the orbits. The protraction phase, which includes the actual swallow, is shown as a dotted line.

anterior to food on its surface. Movement of food is accomplished by pressure between the tongue surface and the palatal mucosa anterior to the food.

In chew cycles with transport, food is moved to the oropharynx, where it is held until the next swallow cycle. In swallow cycles the soft palate is elevated so that it no longer contacts the posterior tongue dorsum. The posterior tongue is elevated and is moved back so that food is pushed further into the oropharynx. Movement of food into the esophagus is achieved by the combined activity of the tongue movements just described and contraction of the pharyngeal constrictors. Anterior movement of the hyoid during the period when food is being moved into the esophagus may represent forward movement of the larynx that has been described for human swallows (Ardran et al., 1951).

The mechanism of transport in primates and nonprimates

The squeezing mechanism of transport that is used by macaques to move food from the oral cavity to the oropharynx is similar to that seen during occasional opossum lapping cycles (Crompton and Weijs-Boot, in prep.), and also during cat lapping cycles (Hiiemae et al., 1978; Thexton, pers. comm.), and during the human swallow (Miller, 1982). However, a different mechanism of intraoral transport is used for solid foods by these animals (reviewed in Hiiemae and Crompton, 1984). Cats, opossums, tenrecs, and hyraxes "pull-back" food with the tongue, rather than squeezing it.

Although both macaques and typical mammals have protract-and-return phases of tongue and hyoid movement, the transport of food occurs at different points in these cycles. Macaques move food from the oral cavity to the oropharynx during the tongue/hyoid protraction phase, which begins either shortly before or at minimum gape, and which continues during the early stages of jaw-opening. The tongue/hyoid protraction phase in hyrax chewing cycles also begins at the same time as the jaw begins to open and, as in macaques, continues through the early part of jaw-opening. However, during the tongue/hyoid protraction phase of hyraxes, food remains relatively stationary. It is held in place by the rugae of the palatal mucosa while the tongue slides forward beneath it. Posterior transport of food is accomplished by hyraxes during the tongue/hyoid return phase. At this time contact between food and the palatal mucosa has been broken. The tongue is retracted and food on the tongue dorsum is thereby moved toward the oropharynx.

An obvious morphologic difference correlated with the mechanism of transport is the presence and degree of development of palatal rugae. In the hyrax (Franks and German, in prep.), the opossum (Crompton and Weijs-Boot, in prep.), and the cat (Thexton, pers. comm.), the rugae of the palatal mucosa are prominent ridges. In macaques the subpalatal mucosa is relatively smooth. The relationship of rugae to method of transport is shown in Table 1. Animals with smooth palates never use the pull-back mechanism for Stage II transport. Animals with pronounced rugae use the squeeze method for liquid food but use pull-back for solid food.

The nature of rugae in mammalian neonates varies (Linden, 1905). Many, such as oxen and sheep, have fully adult rugae at birth. Others, such as dogs, have reduced rugae at birth and develop them about the time the molar teeth erupt (Linden, 1905). If neonates use the squeeze mechanism or some variant of it, one could predict that as adult rugae appear a switch occurs to a pull-back mechanism of food transport. A corollary of this reasoning is that retention of a smooth palate is a neotenic trait of the anthropoids.

Another difference between anthropoids and other mammals lies in the anatomy and the use of the oropharynx. In macaques only small amounts of food are stored in the oropharynx before a swallow moves that food into the gut. Hyraxes store food in the oropharynx and vallecular regions for 20 or more chew cycles before they swallow. The morphologic basis for this difference is the much reduced vallecular area in macaques, compared to nonanthropoid mammals, so that less food can be stored prior to swallowing.

TABLE I. Palate type and mechanism of transport of some mammals

Palate type	Transport Mechanism: Liquid food	Transport Mechanism: Solid food	Adult palate	Neonate palate
Smooth	Squeeze	Squeeze	Man Macaque	Man Dog Macaque
Rough	Squeeze or flow	Pull-back	Cat Dog Opposum Hyrax	Oxen Sheep

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