

Feeding in Golden Hamsters, *Mesocricetus auratus*

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ABSTRACT Simultaneous cine and electromyographic records of freely feeding, unanesthetized golden hamsters show that their motion and muscular activity during mastication differ from those of albino rats (Weijs, '75). Rats show only propalinal motion while hamsters show lateral translation as well. The masticatory muscles of hamsters and rats are generally similar, but their molar dentitions differ. The interlocking molar cusps of hamsters restrict propalinal protrusion and retrusion when the molars are in occlusion; however, hamsters readily unlock occlusion by a twisting movement in the horizontal plane. Rats may perform propalinal movements even with the teeth in occlusion.

In mastication the hamster's jaw moves laterally as well as vertically and anteroposteriorly. Chewing orbits typically reverse after one to three orbits. Reversal begins at the start of the upstroke and involves a lateral shift in the opposite direction with the mouth closed.

Electromyograms show that symmetric and asymmetric activities of closing protrusive and closing retrusive muscles produce a unilateral force couple on both sides. (This couple accompanies a midline closing stroke.) When the mouth is closed, unilateral activity of closing retrusors and closing protrusors also induces lateral translation. A bilateral force couple pits the retrusors of one side against the protrusors on the opposite side. Simultaneous with lateral excursion to the opposite side of midline and the action of these closing muscles, the anterior digastric and lateral pterygoid muscles of one side fire asymmetrically.

The mandible moves downward coincidentally with bilateral activity of the digastrics and lateral pterygoids. As the jaw opens further, activity differences of the lateral pterygoids accompany a shift of the mandible toward midline. At the end of the downstroke, all masticatory muscles studied are silent. The jaw returns to midline when the adductors fire asymmetrically at the start of closing.

Trituration appears to coincide with an initial simple protrusion, which is subsequently accompanied by lateral translation. Different food types are reduced by distinct chewing patterns with the differences clearest when the teeth are near occlusion. During gnawing the lateral pterygoids and digastrics fire longer, and the closing muscles fire less strongly. Chewing patterns in golden hamsters appear more generalized than those of rats; the differences may be directly associated with the ability of hamsters to store food in their cheek pouches.

Much of our present understanding of the function of the mammalian masticatory system has been based upon comparative anatomical studies of teeth, skulls and masticatory musculature (cf. Arendsen de Wolff-Exalto, '61; Becht, '53; D'Amico, '65; Hiiemae, '67; Smith and Savage, '59; Turnbull, '70). Extrapolation from such structural data has allowed diverse masticatory processes to be subdivided into general and specialized pat-

terns (Turnbull, '70). Although aspects of this classification are certainly still open to question (Crompton and Hiiemae, '70; Kallen and Gans, '72), it is clear that rodents show one of the extremes of modifications in their masticatory apparatus. Accordingly, further information about diverse rodents should enhance

¹This study is part of my dissertation research which was conducted at the Department of Anatomical Sciences, The State University of New York at Buffalo.

our understanding of the masticatory process generally (Gans, '66a). Mastication has already been studied in the laboratory rat, *Rattus norvegicus albinus* (Hiimeae and Ardran, '68; Weijs, '75; Weijs and Dantuma, '75) and is now being investigated in guinea pigs (de Vree, '77). The present work deals with mastication in another myomorph rodent, the golden hamster, *Mesocricetus auratus*.

The comparative morphology of teeth has received the greatest emphasis thus far. Wear patterns on the occlusal surfaces of the dentition are assumed to reflect the path of masticatory movements (Brodie, '34; Butler, '56; Fox, '65; Mills, '67; Peyer, '68; Ryder, 1878). In rodents the configuration of the cheek teeth (molars) varies considerably; some show a low brachyodont form and others have more prominent conical cusps (Peyer, '68). These differences in their molar dentition suggest that rodents might show chewing strokes ranging from a simple translational motion (in frontal view) to more elliptical orbits. The molar dentitions of hamsters and rats differ markedly. For these reasons, hamsters were chosen to test the current hypotheses of masticatory patterns.

While the anatomy of the masticatory system, feeding behavior, and diet may differ (Walker, '64), mammalian masticatory motions generally incorporate a lateral component. Domestic rabbits (Ardran et al., '58; Ardran and Kemp, '60), ungulates (Becht, '53; de Free and Gans, '76; Herring and Scapino, '73; Hildebrand, '37; Ryder, 1878; Smith and Savage, '59), little brown bats (Kallen and Gans, '72), rhesus monkeys (Luschei and Goodwin, '74), and American opossums (Crompton and Hiimeae, '70) all show lateral translation during mastication. Distinct feeding habits, such as pouching in hamsters (i.e., the process of storing food in its cheek pouches), may modify chewing strokes among rodents with generally similar anatomy.

We now have studies (Crompton et al., '77; De Vree and Gans, '76; Herring and Scapino, '73; Kallen and Gans, '72; Luschei and Goodwin, '74; Weijs and Dantuma, '75) in which jaw movement and electromyograms of the masticatory muscles have been recorded simultaneously. In bats (Kallen and Gans, '72) the muscles of both sides are generally active during different times of the masticatory cycle. In contrast, rats (Weijs and Dantuma, '75) have bilaterally symmetrical activity of all masticatory muscles. Symmetric activities of

the masticatory muscles (as in rats) tend to move the jaw in the sagittal plane. Asymmetric activities, which couple protrusive forces of one side with retrusive forces of the other, apparently induce (as in bats) lateral translations of the mandible.

Even though the masticatory muscles of golden hamsters and albino rats (Weijs, '75) have a similar gross configuration, the animals show different molar dentitions and masticatory movements. The present analysis of golden hamsters extends beyond the description of their jaw movements during chewing and examines aspects of gnawing and pouching. It also considers whether mastication occurs simultaneously on both sides, or if each cycle involves chewing on one (the active) side only.

MATERIAL AND METHODS

Adult golden hamsters (*Mesocricetus auratus*), members of a colony bred originally from five animals in the functional morphology laboratory at Buffalo, were studied. Morphology of the teeth and the bony configuration of the jaws and mandibular fossae were described from four skulls. The temporomandibular joints and masticatory muscles were described after dissection of twelve preserved heads. Heads of two freshly sacrificed animals were stored overnight in 80% alcohol and then dissected; another specimen was dissected without preservation. Muscular morphology was confirmed during routine autopsies of the 30 hamsters used for electromyography.

All gross observations were made under a Wild dissecting microscope at magnifications between $\times 3$ and $\times 25$. Drawings were made with a Wild camera lucida, and photographs were taken with a Miranda SLR 35 mm camera.

Masticatory muscles were dissected in layers to note sites of muscular attachment. The temporalis and digastric muscles became visible immediately after removal of the skin. Exposure of the masseteric complex entailed anterior retraction of the overlying cheek pouch. The pterygoid muscles were exposed by removal of the tongue, pharynx, and hyoid musculature; the digastrics did not have to be removed to obtain adequate exposure of the pterygoids. Tissues were moistened with distilled water to facilitate the separation of muscles along fascial planes.

Dissected temporomandibular joints were examined for the relative thickness and loca-

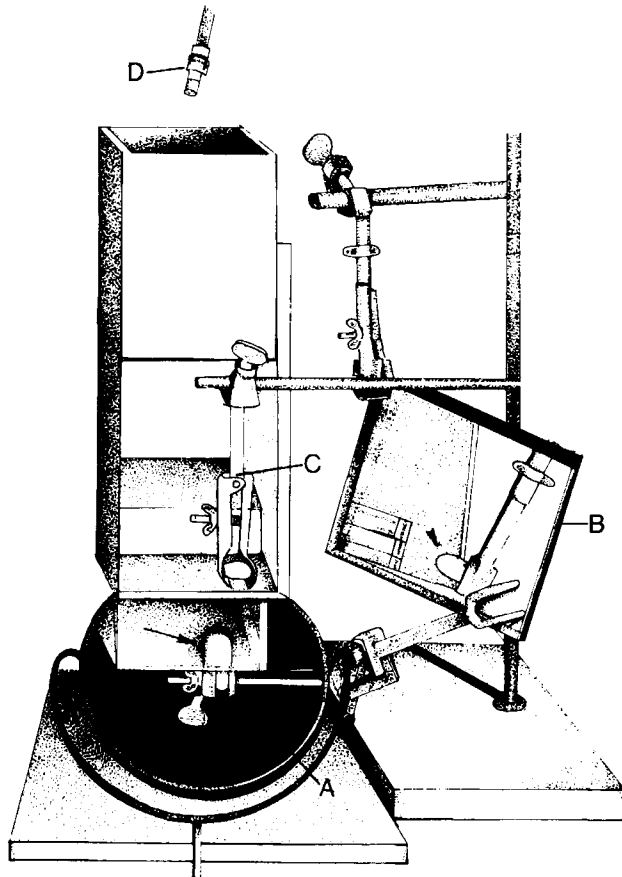


Fig. 1 Diagram of feeding enclosure used in this study. A. Mirror used to record frontal views of masticatory movements. The anterior plexiglas shelf and bottom of a laboratory pellet (arrow) are shown in reflection. B. Mirror used for simultaneous lateral cine views. The side of the pellet (arrowhead) is seen through a plexiglas plate on that side of the enclosure. C. Test tube clamp used to hold pellet. D. Miniature connector (male) suspended above open top of cage.

tion of capsular ligaments, the passive limits of mandibular motion during vertical, horizontal and propropalinal excursions, and the degree of rotation permitted about the long axes of the mandibular bodies (i.e., the amount of spread permitted between the tips of the lower incisors). Similar passive manipulations were performed on three anesthetized hamsters. Capsules were also incised horizontally around the anterior and lateral aspects of the condylar neck to examine the configuration and limits of the articular disc.

Heads of three freshly-killed hamsters were fixed in 10% formalin: one with the mouth closed, another near mid-opening, and a third at maximum gape. Each head was split sagittally and then x-rayed with a Universal dental

x-ray machine (filters removed) for 20 seconds at 10 milliamperes. The positions of the condyle and teeth were recorded in all three specimens.

Thirty conditioned hamsters were fed separately in a shielded enclosure (18 cm × 9 cm × 23 cm) in which the floor was elevated 5 cm above an anterior plexiglas shelf and one side walled off by a vertical plexiglas window (fig. 1). Mirrors, placed respectively below and to one side of the viewing partition, were adjusted to show simultaneous anterior and lateral views of the head. Sunflower seeds and laboratory pellets coated with sugar water (Charles Rivers maintenance formula) were offered. The pellets were held above the anterior plexiglas shelf by a test tube clamp (fig. 1).

Frame-by-frame analysis of cine films used the lower incisors as indicators of mandibular movement. Actual point by point plotting of a complete chewing cycle becomes less accurate when the mouth is closed; the lower incisors are then hidden from view by the lower lip and overriding upper incisors. Hence, a 6-mm-wide anterior segment of the lower lip was removed surgically two to three days before 19 experimental sessions. Neither control motion picture sequences nor direct observations revealed significant change in hamster feeding behavior after removal of the lower lip or surgical implantation of electrodes for electromyography. Eight unoperated hamsters were filmed (as controls) during chewing and gnawing and five while pouching foods of different size. These records made it easy to distinguish gnawing and pouching behavior from chewing in subsequent electromyographic and movement analyses.

An average dose of 0.3 ml nembutal sodium (50 mg/ml) was administered intraperitoneally for all surgical procedures. The ventral and lateral surfaces of the mandible as well as an area from behind the eyes to the scapular region were cleared of hair with a depilatory lotion ("Neet," Whitehall Laboratories, New York, New York). All electrodes were implanted through incisions, and most muscles were exposed directly. Implantation into the digastrics, medial and lateral pterygoids, and the masseteric complex occurred through a 1-cm ventral incision along the side of each mandibular body. Medial retraction of the digastric permitted direct observation of the medial pterygoid. Posterior retraction of the medial pterygoid exposed the lateral pterygoid muscle. Electromyographic sequences from the muscles, which had been retracted during surgery, showed no detectable change from those of the non-retracted muscle in the same or other animals. Electrodes were placed blind within the deep masseter and anterior zygomaticomandibularis muscles by passing the needles, respectively about 1 and 1.4 cm, upward and rostrally through the superficial masseter. No significant change in superficial masseter activity was noted as a result. The anterior and posterior temporales of both sides were exposed through a 1.5-cm midline incision along the dorsum of the head. Electrodes were placed in the deep temporalis through an incision along the upper posterior margin of the zygomatic arch; the needle was passed

parallel to the root of the arch and through the posterior temporalis until it contacted the lateral cranial wall. The tip of the needle was then pushed about 0.5 cm upwards and anteriorly along the bone toward the middle of the eye.

Four to eight electrodes were ordinarily implanted (and color coded) during a single surgical procedure. Bipolar electrodes of 0.003-inch teflon-coated silver wire (Medwire Corp., Mt. Vernon, New York; most muscles) and 0.0009-inch "karma green" wire (Driver-Harris Corp., Harrison, New Jersey; lateral pterygoid and deep temporalis) were used to record intramuscular electrical activity. Electrode wires were kinked two or three times near their point of emergence from a muscle, forming them into springs and thereby facilitating their intramuscular retention. Each electrode pair was passed from the surgical incisions through a 15-gauge hypodermic needle that had been inserted from a site between the scapulae and run under the skin, superficial to the cheek pouches. The bared free ends of the electrodes were soldered to a harness of lightweight earphone wire (Audio Center, Buffalo, New York) collected at an Amphenol connector and insulated with appropriately color coded electrical tape. The connections were fastened to the animal's back and coated with a noxious solution used to prevent nail-biting in humans (Stop-Zit, Purepec Corp., Elizabeth, New York). The connector was suspended from the open top of the holding cages. Recording sessions always started more than 24 hours post-operative in order to permit complete recovery from the anesthesia.

Two different electrode configurations were used. The first (fig. 2 top) is that described by Kallen and Gans ('72). In order to guard against shorting out (by contact) of the electrode tip, it was modified slightly. The bared tips were of equal length: one millimeter on the Karma electrodes and two millimeters on the silver. The wire was looped in the middle and the limbs of the loop twisted five or six times. One to two millimeters of insulation were removed on one side of the loop, just distal to the twist. One-half of this bared length was twisted again, around the other insulated limb of the loop. For the other tip, a section of insulated wire was left intact, distal to the twist and equal to the bared untwisted area already exposed. The second end was then bared distal to this insulation and both elec-

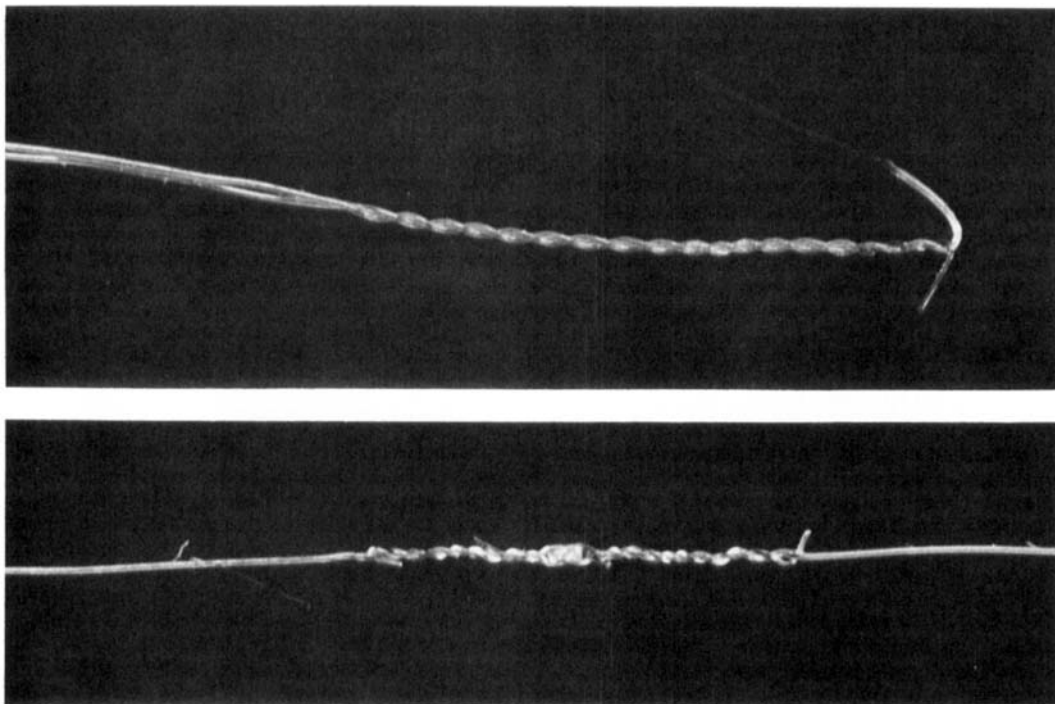


Fig. 2 Photograph of electrodes used in this study.

Top Injection type electrode made of 0.003-inch teflon coated silver wire.

Bottom Pass through electrode formed from 0.003-inch teflon coated silver wire.

trode tips bent backwards at the distal end of the twist. The silver electrodes were inserted with 26-gauge needles and the Karma wire with 27-gauge.

A second electrode configuration (fig. 2 bottom), formed from the 0.003-inch silver wire solely to record activities from the anterior digastric muscles, was needed to retain electrodes in these muscles. Two separate lengths of wire were tied together with a square knot, leaving two short free ends. Two millimeters of insulation were removed from each short end, close to the knot, and each bared length was twisted completely about its respective, longer insulated segment. One end of the electrode was threaded into a curved, hubless, 26-gauge hypodermic needle that was passed completely through the muscle, implanting the twisted portion of the electrode.

Some motion picture sequences were recorded on Kodak Ektachrome EF daylight film at 33 and 64 frames per second with a Beaulieu R16 camera using two Color-Tran narrow beam spotlights. Individual frame identifica-

tion was provided by a notched metal disc, mounted on the externally-located sound synchronization shaft of the camera. This disc was located in front of a prefocussed light source, and the notch permitted a pulse of light to pass through an optical fiber to the face of the oscilloscope screen. A similar optical fiber arrangement displayed 1-second time intervals. Both ends of these optical fiber bundles were flattened to enhance the amount of light transmitted and the end at the oscilloscope screen was bent at right angles to face the camera. All available channels on the Tektronix 535A oscilloscope with type M plug-in unit could then be used for simultaneous recording of electromyograms. Traces were photographed on Kodak 2495 RAR film with a Grass C4 camera run at 100 mm/sec with continually open shutter. Other experiments employed a Beaulieu R16 camera with strobe illumination and a photocell providing a signal for individual film frame identification (Gans, '66b). Up to eight electrode signals were amplified through four 26A2 and/or four FM

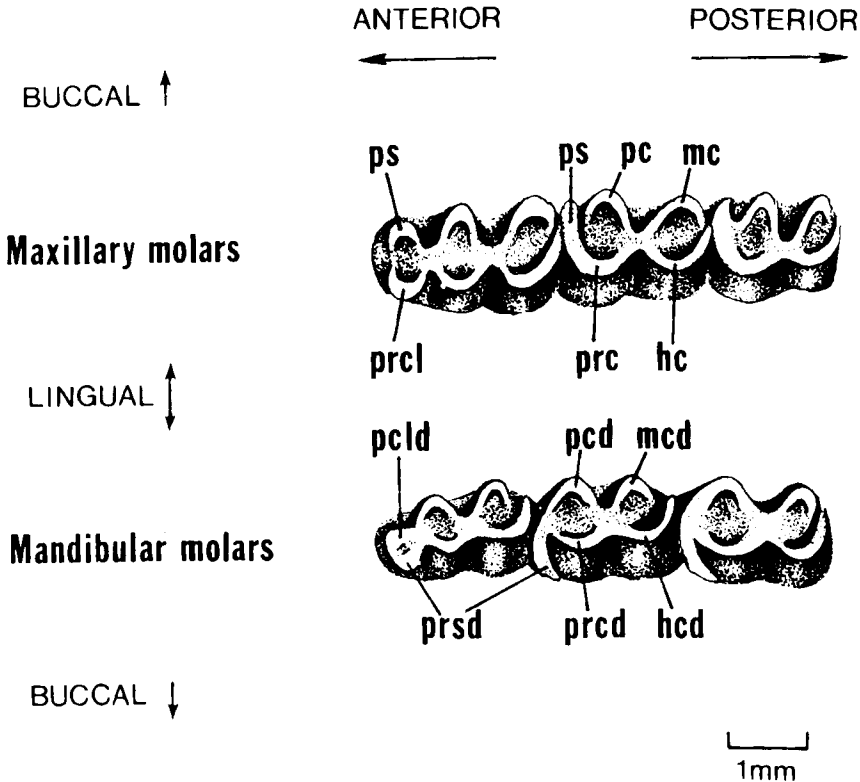


Fig. 3 *M. auratus*. Molar dentition. The occlusal surfaces of the right side of the specimen are shown. Hc, hypocone; hcd, hypoconid; mc, metacone; mcd, metaconid; pc, paracone; pcd, paraconid; pcd, paraconulid; prc, protocone; prcd, protoconid; prcl, protoconule; prsd, protostylid; ps, parastyle. (Nomenclature of Osborne, cf. Kraus et al., '69). With the teeth in occlusion, the protoconid of the second mandibular molar fits just mesial to the paracone of the second maxillary molar overriding the parastyle. The metacones of the first and second upper molars lie in the groove just distal to the respective hypoconids, overriding the protostylids of the second and third mandibular molars. The paraconids of the second and third mandibular molars fit lingually between the adjacent boundaries of the first and second, and second and third maxillary molars respectively.

122 Tektronix preamplifiers, monitored on a Brush 481 strip chart recorder and a Tektronix 565 oscilloscope, and stored for later use on a Honeywell 5600 medium bandpass, multi-channel tape recorder.

Electromyograms from a given hamster could be recorded daily for up to five days, but experiments usually ran for three days. Each animal was then sacrificed with ether and autopsied to determine the exact placements of the electrodes (figs. 6-8).

A W/R analytical motion picture projector was used to analyse mandibular movements and plot orbits from frontal and lateral views. As the teeth were incompletely and variably exposed throughout the orbit, even in animals with segments of the lower lip removed, it proved necessary to use different reference points for different portions of the orbit. Rela-

tive positions of maxillary incisors (when exposed) were cross checked with those of the nostrils and upper end of the median cleft of the upper lip. In animals with a segment of lip removed, the point at which the cleft, between the lower incisors intersects the gingival margin, was employed in frontal view for all except the one or two frames showing maximum gape when this reference point was nearly horizontal. This point was approximated by plotting the cleft between the tips of the lower incisors. In animals with intact lips, the middle of the lower lip was used for all frames except the one or two at maximum gape when the cleft between the incisal tips was again used. For lateral views, the point where the anterior aspect of the chin meets the lower border of the jaw was the landmark.

Actual displacements were measured from a

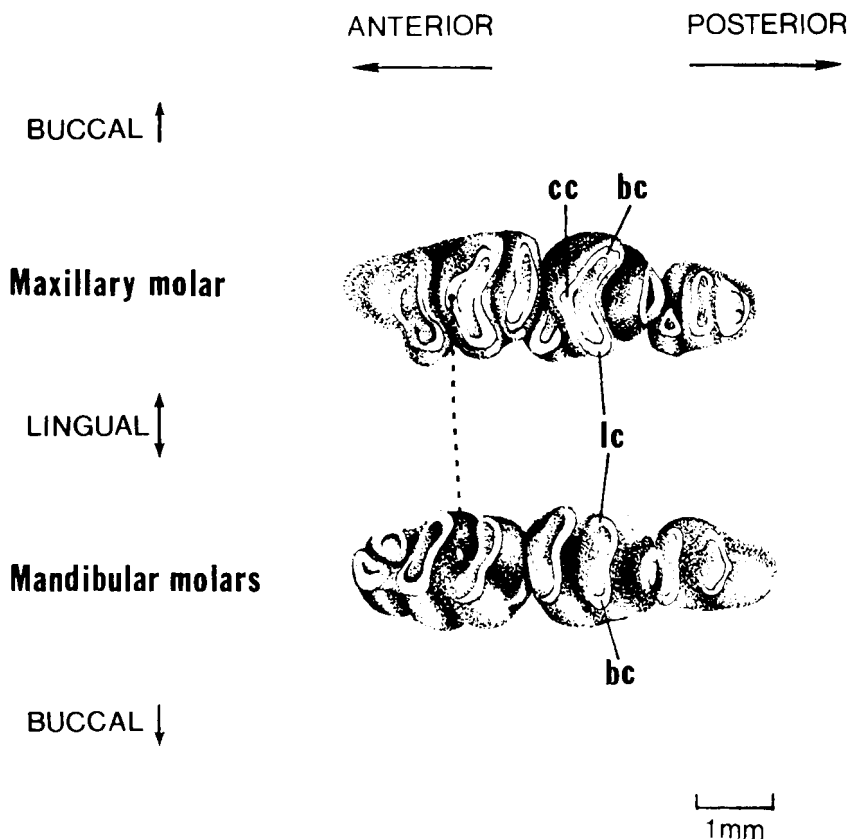


Fig. 4 Camera lucida drawings of the occlusal surfaces of the right molar dentition from a young albino rat (*Rattus norvegicus albinus*). bc, buccal cusp; cc, central cusp; lc, lingual cusps. The broken line connects the central cusp with the respective fossa into which it lies when the teeth are in occlusion.

millimeter scale photographed at the start of each session. Vertical, horizontal, and propalinal components of motion were plotted as displacements, velocities, and accelerations. Movement analysis first determined individual orbital patterns, then sequential patterns of masticatory orbits and patterns of reversal in direction and side preferences.

Electromyograms were analysed for the start and stop of muscle activity and changes in relative firing amplitude. Twenty sets of electromyograms were analysed in detail with good simultaneous cine. Further information was gained from other sequences of electromyograms without cine by cross correlation with one or more muscles recorded previously from simultaneous records.

RESULTS

Anatomy

The morphology of golden hamsters is pre-

sented in comparison to published data for laboratory rats (Weijs, '73, '75; Weijs and Dantuma, '75), with emphasis upon differences between them.

The molar cusps of hamsters show a tribosphenic pattern. The cusps are named according to the system of Osborn (cf. Kraus et al., '69; Romer, '70) in which the major cusps are designated by the suffixes -cone, or -conid, and the minor cusps by the suffixes -conule, -style, or -stylid. The terminology of Weijs ('75) is followed for rat molars.

The molars of hamsters resemble each other much more closely than do other molars characterized as tribosphenic (cf. *Myotis*; Kallen and Gans, '72). All molars have four conical major cusps, which show no marked antero-posterior slant, and one minor cusp. An additional minor cusp is present on the first molar. The major cusps lie on the lingual and buccal borders of the molars with the lingual cusps

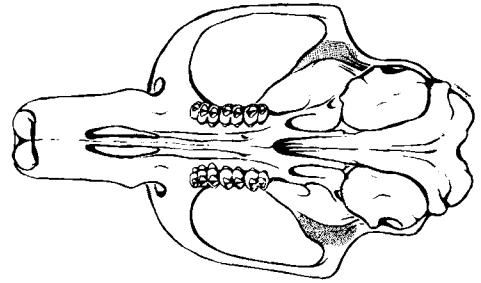
situated anterior to their corresponding buccal cusps (see fig. 3 for the cuspal arrangement of the molars and their interdigitating pattern).

In contrast, the unworn molars of young rats (about 3 months old) show low transverse ridges extending across the occlusal surfaces. These flattened grinding surfaces face posteriorly on the upper molars and anteriorly on the lowers. In general, the maxillary molars exhibit a central, buccal, and lingual row of cusps in the long axis of the tooth-row and the mandibular a buccal and lingual row (fig. 4). The transverse ridges of the lower cusps are depressed centrally and form a trough that provides an anteroposterior guide for the central cusps of the maxillary molars.

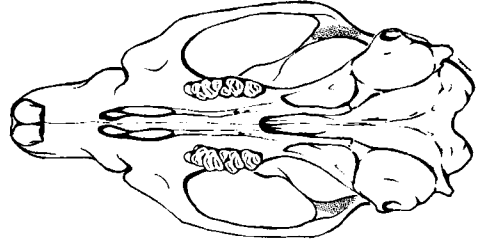
The upper and lower tooth-rows of hamsters and rats are isognathous. When the tips of the lower incisors are pressed together, the lingual and buccal borders of the respective molars are approximated in hamsters. In rats, the buccal borders of the mandibular molars are lateral with respect to the maxillary. In both rodents, the maxillary tooth-rows slant outward from midline and the mandibular inward, but the degree of slanting is greater in hamsters. Thus, the occlusal planes of hamsters incline further inward from horizontal than in rats.

Although the incisors are longer in rats, they are nearly the same length in both rodents in relation to mandibular length. The robust lower incisors of hamsters curve upward more sharply than those of rats and the respective tips of the upper and lower teeth lie nearly parallel in hamsters. The worn posterior incisal surfaces of rats are flat, but they are concave in hamsters. From the front, the cutting edges of the incisors are flat and distinctly chisel-shaped in hamsters, whereas those of rats are tapered and rounded.

Full occlusion in hamsters shows the cusps of the upper and lower molars tightly interlocked. The major mandibular cusps fit anterior (medial) to their corresponding cusps of the maxillary molars (fig. 3). The major buccomesial cusps of the second and third lower molars articulate over the minor cusps of the second and third upper. In turn, the bucco-distal cusps of the first and second maxillary molars override the minor cusps of the second and third mandibular molars. The paired minor cusps of the first lower molars lie anterior to those of the upper first molars.



A



B

Fig. 5 Diagrammatic ventral view of the skull of a hamster (A) and an albino rat (B). In both, the mandible has been removed *in toto*. The stippled areas show the extent of the mandibular fossae. See text.

In occlusion, the lower incisors of hamsters lie on midline, with the tips nearly abutting the lingual base of the upper incisors. The condyles lie in a single transverse plane, each in the posterior portion of the mandibular fossa and midway between its medial and lateral bony boundaries.

When the teeth of rats are occluded, the mandibular buccal and lingual molar cusps lie anterior to their corresponding maxillary cusps. The central cusps of the maxillary molars fit inside the borders of the buccal and lingual mandibular cusps (fig. 4). The tips of the lower incisors are spread apart and well posterior to the lingual base of the uppers. Each condyle in rats lies in the posteromedial portion of its mandibular fossa.

Mandibular manipulations of hamsters reveal that the easiest way to unlock molar occlusion is by twisting the jaw about a vertical axis so that one condyle slides forward and the other backward. On the side of forward condylar excursion, the mandibular cusps move mesio-lingually, while those on the opposite side move disto-buccally. Thus, the lower incisors shift laterally from the midline to the side of

TABLE 1

Muscles	Origin	Insertion	Motions induced		
			Vertical displacement	Lateral translation	Antero-posterior translation
Lateral pterygoid	Lateral surface of lateral pterygoid plate maxilla posteromedial to the third upper molar	Medial side of condylar neck, joint capsule, and articular disc	Open	Lingual	Protrusion
Medial pterygoid	Lateral surface of medial pterygoid plate, pterygoid fossa, medial wall of lateral pterygoid plate	Fossa on medial side of angular process, forms muscular sling with superficial masseter	Close	Lingual	Protrusion
Diagistric					
Anterior belly	Rostral end of posterior belly via a raphe	Ventromedial border of the body of the mandible as far as symphysis	Open	Lingual	Retrusion
Posterior belly	Paroccipital process	Caudal end of anterior belly via a raphe	Open	Lingual	Retrusion
Masseter					
Superficial head	Anterosuperior to first maxillary molar, lateral aspect of zygoma	Ventral and lateral surfaces of angular process, ventromedial body inferior to medial pterygoid insertion	Close	Lingual	Protrusion
Deep head	Lateral border of zygoma, orbital portion of maxilla, anterosuperior to infraorbital foramen between maxillary and premaxillary suture	Superior surface of angular process, masseteric ridge	Close	Lingual	Protrusion
Zygomatocmandularis					
Infraorbital head	Maxilla anterior to infraorbital foramen	Joins the deep rostral fibers of anterior head to insert on mandibular ramus	Close	Lingual	Protrusion
Anterior head	Medial aspect of zygoma	Anterolateral border of ramus of the mandible superior to insertion of deep masseter	Close	Lingual	Protrusion
Posterior head	Posteromedial border of zygomatic arch	Ventrolateral surface of condylar process of mandible, separated from anterior head by masseteric nerve	Close	Lingual	Retrusion
Temporalis					
Anterior head	Mid-sagittal crest, occipital ridge, lateral and anterolateral surface of cranial wall, forms posterior boundary of orbit	Rostral and anteromedial surface of ramus of mandible	Close	Buccal	Retrusion
Posterior head	Sagittal and lamboid crest, squamosa of temporal bone	Superior and lateral aspect of coronoid process	Close	Buccal	Retrusion
Deep head	Lateral cranial wall deep to posterior head	Medial surface of coronoid process	Close	Buccal	Retrusion
Suprazygomatic head	Rostral surface of zygomatic process of temporal bone	Lateral aspect of coronoid process directly below insertion of posterior head	Close	Buccal	Retrusion

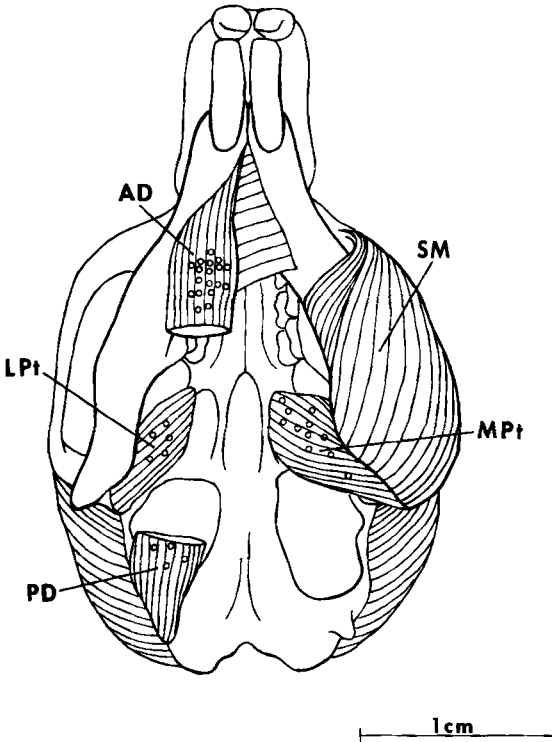


Fig. 6 *M. auratus*. Diagrammatic ventral relationships of the medial (MPt) and lateral (LPt) pterygoid muscles from camera lucida tracings. The right side of the figure shows a superficial exposure and the left a deeper dissection. Only the central portion of the digastrics have been removed on the left, leaving the bony attachments of the anterior (AD) and posterior (PD) bellies intact. The right digastric has been removed *in toto*, as well as the superficial masseter (SM) and the left medial pterygoid. The circles superimposed are electrode placements. In the anterior digastrics only, actual electrode location have been spread out slightly to show the number of placements more clearly.

backward condylar movement. When the teeth are occluded, neither anteroposterior nor transverse movements occur as the cusps interfere. Rotation of the mandibles about their long axes binds the interdigitated cusps and restricts subsequent twisting of the mandible about a vertical axis. In contrast, the occluded molars of rats permit anteroposterior movement. The central cusps of the maxillary molars pass through the the longitudinal trough of the mandibular molars. However, the buccal and lingual cusps restrict transverse movements and rotation about a vertical axis.

In hamsters, the incisors are brought into a gnawing position from molar occlusion by a downward and anterior movement of the man-

dible. This movement terminates when the mesial borders of the first lower molars lie about half a molar length anterior to the mesial borders of their upper counterparts, and the condyles lie in the anterior portion of the mandibular fossae. In rats, a gnawing position is obtained by an anterior and inferior movement, with the lower jaw first moved anteriorly. The first mandibular molars of rats lie entirely rostral to the first maxillary molars.

The skull of adult hamsters is shorter and stouter than that of adult rats. In hamsters, the zygomatic arch curves sharply outward, extending further laterally from the mandibular fossa than does that of rats (fig. 5). From the side, the zygoma of hamsters are straight and high on the skull.

In hamsters, the distal end of the mandible curves upward more sharply than that of rats, and the mandibular ramus is narrower and the masseteric ridge less pronounced. In both rodents, the rostral tips of the lower jaws are joined by a plate of fibrous connective tissue, which permits flexibility at the symphysis menti (cf. Scapino, '65, for *Canis*). The mandibular ramus of hamsters diverges well lateral to the lower molar tooth-row, whereas the ramus of rats is nearly parallel to its molars. The angular process is prominent in hamsters. The inferior border curves sharply inward, forming a deep fossa on the medial surface for the insertion of the medial pterygoid muscle. The coronoid process of hamsters is long, slender and curves more caudally than in rats. In both animals, the condyles lie at the same relative distance above the occlusal surface of the upper molar tooth-rows, but those of hamsters curve inward. As a result, the coronoid and angular processes of hamsters are relatively more lateral to the condylar head than those of rats.

Fig. 7 *M. auratus*. Diagrammatic lateral view of the muscles of mastication based on camera lucida tracings.

A Superficial view shows the masseter, temporalis, and posterior digastric muscles.

B The deep masseter has been fully exposed by removal of the superficial head.

C The divisions of the zygomaticomandibularis muscle are seen following the removal of the deep masseter. The anterior digastric is also shown. AD, anterior digastric; AT, anterior temporalis; AZM, anterior zygomaticomandibularis; DM, deep masseter; IO, infraorbital portion of the zygomaticomandibularis; MPt, medial pterygoid; PD, posterior digastric; PT, posterior temporalis; PZM, posterior zygomaticomandibularis; SZT, suprazygomatic temporalis. The circles superimposed are electrode placements.

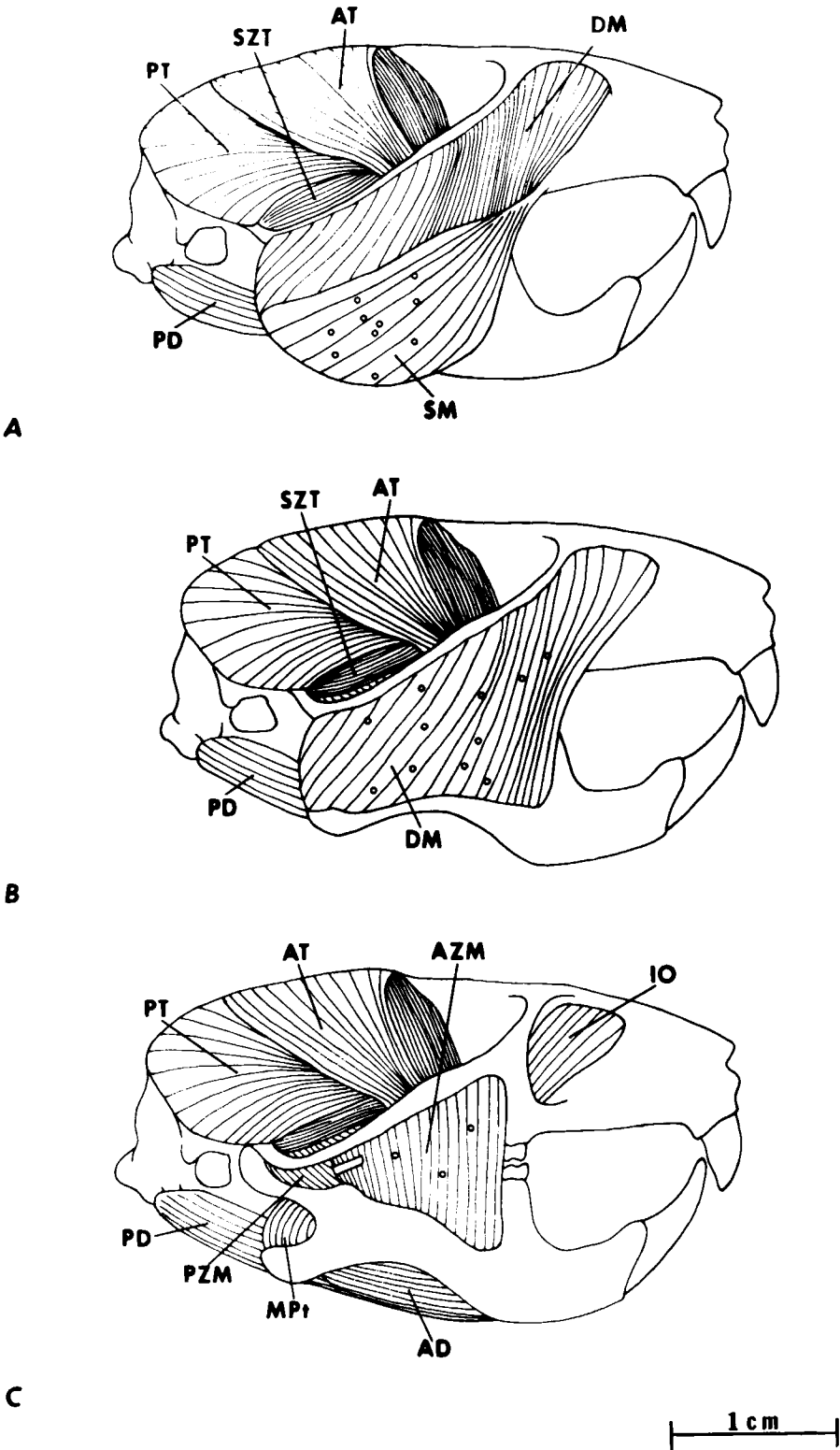


Figure 7

The mandibular fossae in both rodents (fig. 5) are bounded medially by the tympanic portion of the temporal bone and laterally as well as superiorly by the root of the zygoma; the anterior and posterior ends are free of bony boundaries. In hamsters, the posteromedial walls of the fossae are nearly parallel to each other and the base of the skull, but the anteromedial walls slant inward and upward. Laterally, the main bony restriction to condylar movement is formed by the zygoma, which curves sharply outward along the central portion of the fossa. Only low bony ridges extend rostrally and caudally. The width of the anterior portion of the fossa is three-fifths of its entire length, while the posterior portion is two-fifths of that length. The long axes of the deepest parts of the fossae slant anteromedially. In rats, the medial and lateral bony boundaries are nearly straight and parallel to each other with the anterolateral boundary more massive than that of hamsters. The long axes of the rat fossae are nearly parallel and show a slight upward and inward inclination anteriorly. The entire fossa is nearly twice as long as it is wide.

In hamsters, the capsule of the temporomandibular joint loosely encompasses the entire mandibular fossa. Only two major capsular ligaments are seen in an otherwise thin capsule. A stout posterolateral ligament extends from the posterior end of the zygomatic process of the temporal bone and slants rostrally to the caudolateral border of the condylar neck. The other ligament is narrow and extends anteromedially from the rostral border of the (posterior) zygomatic root to the anteromedial aspect of the condyle. Laterally, the joint capsule appears to be fused with the investing fascia of the posterior zygomaticomandibularis muscle and medially with the fascia of the lateral pterygoid muscle. The articular disc is the same size and shape as the mandibular fossa, but it is thinner centrally than peripherally and thickest at the posterior margin.

Passive manipulations of the mandible of dead and anesthetized hamsters reveal a potential for anteroposterior motion, rotation about a vertical axis, and rotation of each mandibular body about its long axis. With both condyles lying at the anterior limit of their fossae, the mandibular molars are nearly one and one-half molar lengths forward of the anterior limit of the maxillary molars, and the lower incisors are rostral to the uppers. In rats

when the condyles lie in the same position, the lower molars are two molar lengths forward of the upper, but the position of the incisors is the same as in hamsters. With the condyles at the posterior limits of the fossae, the mandibular molars of hamsters lie one-half molar length back on the corresponding maxillary molars, whereas in rats there is a full one molar shift. Therefore, the potential range of anteroposterior mandibular excursion appears greater in rats than hamsters. However, reciprocal anteroposterior condylar movement (rotation about a vertical axis) is obtained more readily in hamsters than in rats. In hamsters with the teeth in occlusion or the mandible lowered, the condyle on one side is easily moved to the anterior limit of the fossa and the other condyle to its posterior limit. On the side of the anterior condyle, the molars shift horizontally to lie near the midline of the skull, a distance of one and one-half their molar width. In rats, reciprocal anteroposterior condylar movement to the limits of the fossae is obtained only when the tips of the lower incisors are separated and ventral to those of the upper incisors. In both rodents, rotation about their long axes moves the lower molars less than half a molar width across the uppers.

The gross configuration of the masticatory muscles in hamsters (table 1; figs. 6-8) closely resembles that in rats (Weijjs, '75).

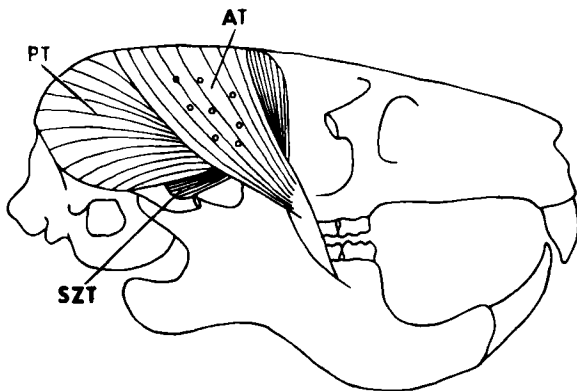
The lateral pterygoid (fig. 6) in hamsters arises from the entire lateral surface of the lateral pterygoid plate, and it appears that the fibers of the lateral and medial pterygoids incline less anteriorly in hamsters than in rats. In hamsters, the long axes of the anterior digastrics diverge more and the posterior digastrics diverge less abruptly than those in rats. Hamsters do not show an anterior medial division of the temporalis; instead, the entire anterior portion of the temporalis has a common tendon of insertion (fig. 8). However, the posterior portion of the temporalis of hamsters may be subdivided into three parts: (1) a posterior head similar to that in rats, (2) a deep

Fig. 8 *M. auratus*. Diagrammatic lateral view of the temporalis muscle based on camera lucida tracings.

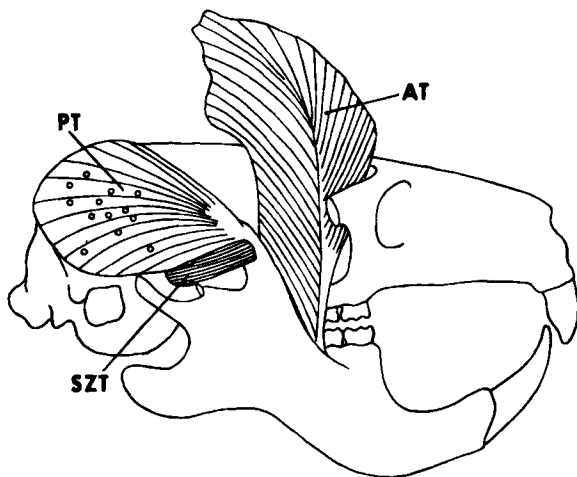
A Superficial view shows the anterior temporalis (AT).

B The posterior temporalis (PT) and suprazygomatic temporalis (SZT) as exposed by rostral displacement of the anterior temporalis (AT).

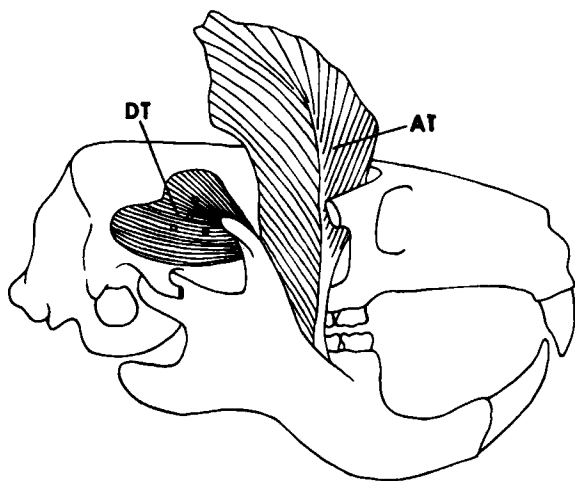
C The deep temporalis (DT) is seen upon removal of the posterior and suprazygomatic heads. The circles superimposed are electrotrode placements.



A

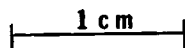


B



C

Figure 8



posterior head which insets on the medial aspect of the coronoid process, and (3) a very small suprazygomatic temporal head, which is adjacent medially to the posterior zygomaticomandibularis muscle and inserts on the lateral surface of the coronoid process.

Lateral x-rays of hamsters, with the molars in occlusion (fig. 9A), show that the condyles lie in the posterior portion of the mandibular fossa with the anterior half of the condylar head medial to the root of the zygomatic arch. The tip of the lower incisor nearly touches the roof of the mouth; a 4-mm portion of the tooth is posterior to the lingual surface of the upper incisor. As the jaw opens by 25° (fig. 9B; the angle measured between the occlusal surfaces of molar tooth-rows), the condyle shifts slightly anteriorly, and the symphysis moves caudally. The tip of the lower incisor is nearly in the same frontal plane as that of the upper incisor. The vertical distances between the occlusal surfaces of the upper and lower molar tooth-rows are 3 mm anteriorly and 1 mm posteriorly, with no marked anteroposterior shift of the lower tooth-row. At maximum gape (fig. 9C; 45° of opening measured as before), the condyle lies in the anterior portion of the mandibular fossa. The lower incisor and symphysis are almost at a right angle to the upper incisors and retruded more than in figure 9B. The vertical separations of the upper and lower tooth-rows are 11 mm anteriorly and 5 mm posteriorly, with the lower tooth-row lying posteriorly by about half the length of the first upper molar.

Feeding behavior

When feeding on commercial hamster pellets and sunflower seeds, hamsters fix these foods with their incisors and forepaws during gnawing. The pellet is of a grainy texture, but the kernel of the seed is soft and covered by a hard shell. Consequently, gnawing behavior differs between pellet and seed.

Gnawing begins with the upper and lower incisors in contact with the food. Pieces of food are freed from the surface of pellets by short, rapid, scraping or chipping movements of the lower incisors. The accompanying jaw movements involve opening protrusion and closing retrusion. The head is held down and the pellet is rotated by the forepaws and incisors to change the point of incisal impact. Feeding behavior is somewhat different when the pellet is mechanically fixed, preventing food rotation. Head turning is more frequent and gnaw-

ing is observed with the head in a more horizontal position. Furthermore, side to side movements of the mandible occur between bites, shifting the contact point between the lower incisors and pellet.

With sunflower seeds, hamsters first remove the shell by crushing it between the incisors. The upper incisors serve as a buttress against one side of the shell while the lower incisors press upward against the opposing surface. Seeds are more frequently rotated (to change the point of impact) than are pellets, but head turning is less frequent with seeds. Portions of the shell are pried away with the incisors and pushed from the mouth by the tongue. Partially consumed seeds show that only part of the kernel is incised. This incised surface is smooth and nearly flat as opposed to the rough and irregular surface left on pellets after gnawing.

The distinct pouching behavior of hamsters differs with the size of the food object. When a large solid mass of food, such as a whole pellet, is pouching, the head is held vertically and moves anteroventrally towards the pellet. As it nears the food, the mouth opens rapidly, positioning the lower incisors nearly at a right angle to the uppers, and the head turns to a more horizontal position. The mouth is then pushed over the pellet, and the food is picked up by the incisors and grasped between the forepaws. Hamsters then use their forepaws to maneuver the pellet to one side of the mouth which will be referred to here as the pouching side. Concurrently, the mandible swings laterally away from the pellet and the pouching side. As the pellet is moved further into the mouth, the top of the head leans towards the pouching side, and the forepaws twist the pellet about its long axis. Gradually, the head moves forward and then downward, so that the mouth is over the pellet. The head continues to move in this direction, even after the food is completely within the mouth, but the forepaws are now rubbed backwards along the outside of the pouch, and the tongue moves in a bucco-posterior direction along its internal

Fig. 9 *M. auratus*. Lateral radiographs of head. The condyles are indicated by arrows.

A Mouth closed. The occlusal relationships are clear for the molars and incisors. Remnants of two electrodes are shown; one in the anterior digastric (bottom) and the other in the temporalis muscle (top).

B Mouth open at 25°. The condyle has shifted only slightly forward.

C Mouth open at 45°. The condyle is well forward in the fossa. Notice the change in the position of the lower incisors in reference to the uppers when the mouth is opened.

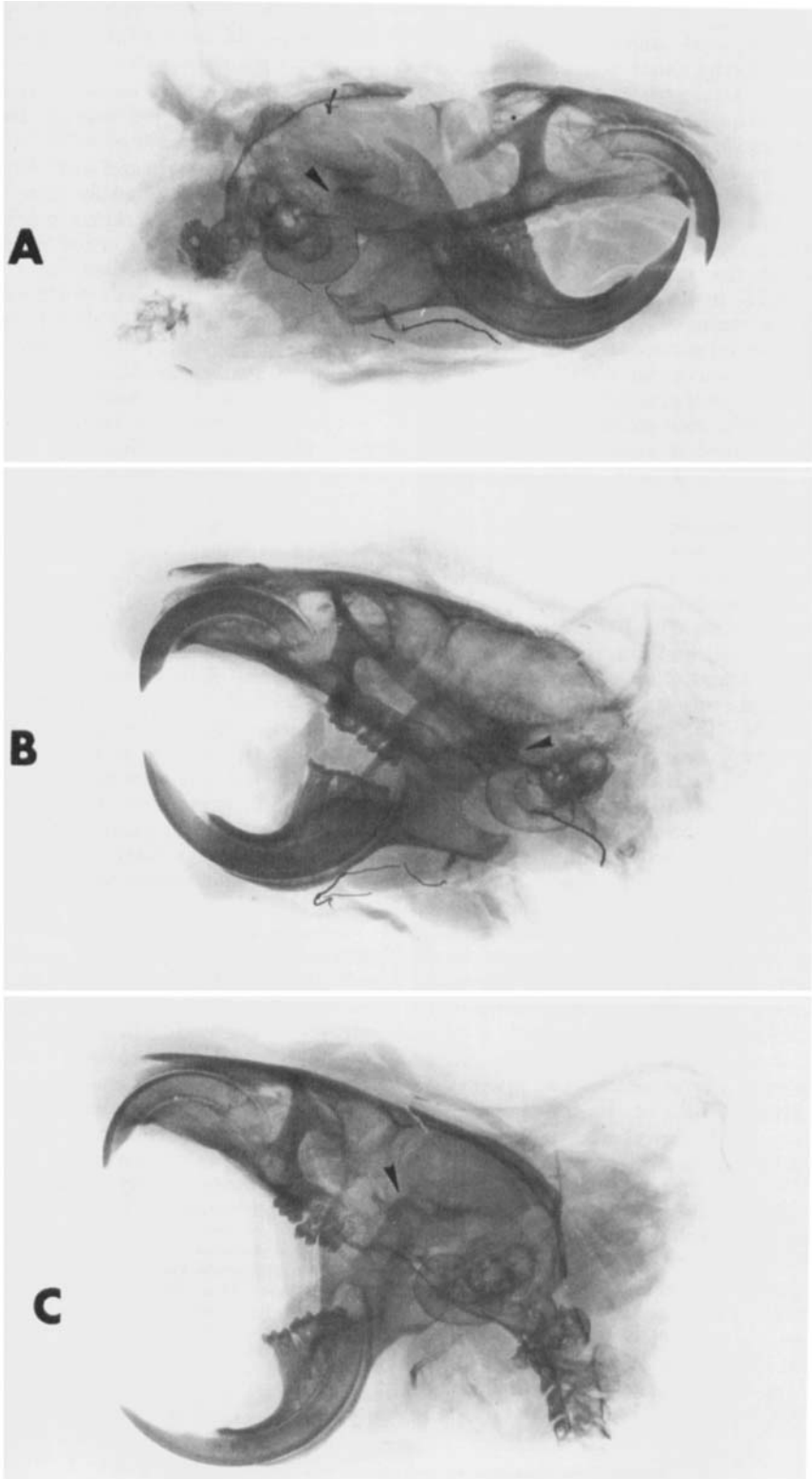


Figure 9

surface. Together, these movements of the head, forepaws, and tongue push the pellet posteriorly into the cheek pouch.

In contrast, hamsters pouching sunflower seeds (one-tenth the size of pellets) seldom use their forepaws. The head is initially held vertically and moved anteriorly and downward towards the seeds. As it approaches the food, the tips of the lower incisors are just below those of the uppers. Seeds are then gathered up by use of the incisors and tongue, and pouched whole, in series, to one side of the mouth. This transfer of seeds appears to involve a repeated posterolateral movement of the tongue, maneuvering the seeds from the incisors to the pouching side. Although the head moves from side to side as well as forward and backward, it moves less when pouching seeds than for pellets, and least during mastication.

The path, described by the anterior tip of the mandible as it moves from a midline closed position, through one opening stroke, and back through one closing stroke, is referred to as a chewing orbit. This (fig. 10) indicates lateral as well as vertical and anteroposterior movements of the mandible. Orbital direction refers to lateral direction taken by the mandible across the top of the orbit.

In frontal view, a typical chewing orbit for pellets (fig. 11A) starts with a lateral shift to one side, after which a vertical movement begins. Next, the jaw opens sharply and, during the downstroke reverses horizontally towards midline. At the wide-open position, the jaw is just slightly to one side or the other of midline. The closing stroke (upstroke) proceeds near the midline and generally starts with a slight lateral shift in either direction. Lateral views (fig. 11B) indicate a strong propalinal component of masticatory motion. However, there appears to be no significant anteroposterior movement as the jaw moves laterally from midline at the top of the orbit. During opening, the orbit curves posteriorly; the rate of its caudal displacement is small at the start but then increases sharply during the lower half of the downstroke. In contrast, the closing stroke follows a relatively straight upward and anterior path.

When sunflower seeds are masticated, the chewing orbit is similar in frontal view. However, lateral excursion from midline at the top of the orbit is typically accompanied by slight opening (fig. 12). Otherwise, orbits for sunflower seeds are the same as for pellets. In side

view, a slight posterior and downward shift occurs during the initial lateral-opening movement.

Hamsters chew both foods at rates between four and six orbits per second. Reversal in orbital direction occurs smoothly after one to three successive orbits and involves a reversal of lateral movement when the mouth is closed. About 10% of all orbits lack a marked lateral component. Such orbits occur randomly and vary in their vertical displacement. Hamsters do not seem to show a side preference, nor do cine records alone supply direct information about an active side. Furthermore, the lower incisor tips remain together during chewing of both food types; no spreading was observed.

Successive orbits do not follow identical paths in frontal view (fig. 13). Their differences are most obvious during the opening stroke. However, these changes (in frontal view) did not consistently relate to changes obtained in lateral views of the masticatory orbits.

Data suitable for analysis of the displacement, velocity and acceleration curves are presently available only for chewing.

The vertical displacement graphs (figs. 14, 15) are derived from frontal views of orbits for seeds and pellets. The graphs peak more sharply at the bottom of the opening stroke than at the top when the mouth is closed. This difference is even more evident for pellets when the top of the graph tends to plateau. Amplitudes of peak vertical displacement are greater and more consistent with sunflower seeds.

Opening and closing vertical velocities for each food (figs. 14, 15) show nearly identical peak amplitudes, although the measured peaks are greater for seeds. Peak opening velocity is reached before peak opening displacement, and peak closing velocity is attained rapidly about midway through the upstroke. Closing velocity then decreases gradually as the jaw continues to close. The rapid change from peak opening to peak closing velocity is more clearly documented in the acceleration graphs. Peak closing accelera-

Fig. 10 *M. auratus*. Frames 101-108 of film showing both frontal and lateral views of the eighth orbit in a masticatory sequence. An anterior segment of the lower lip is removed, exposing the base of the lower incisor. Reproduction from the original color film has resulted in a loss of resolution. Lateral translation during the downstroke and midline closure, however, are seen in frontal view. In lateral view, the tip of the chin displays a reversing posterior and anterior path respectively during opening and closing.

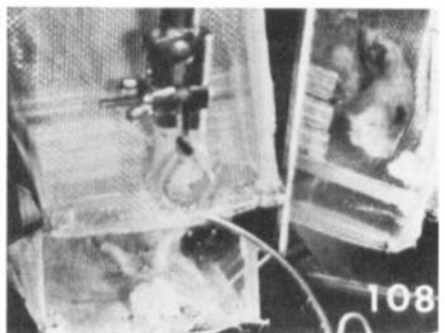
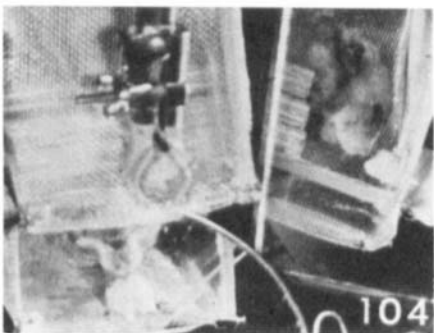
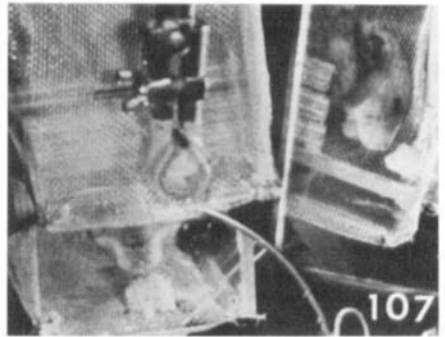
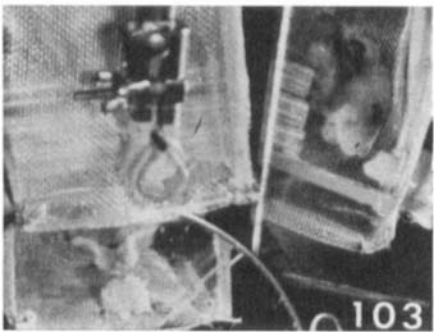
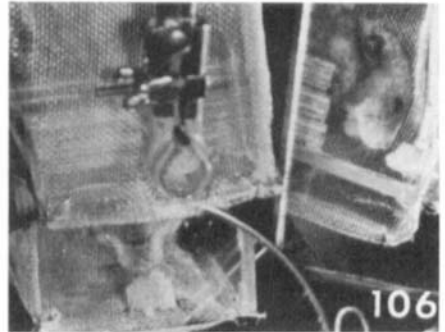
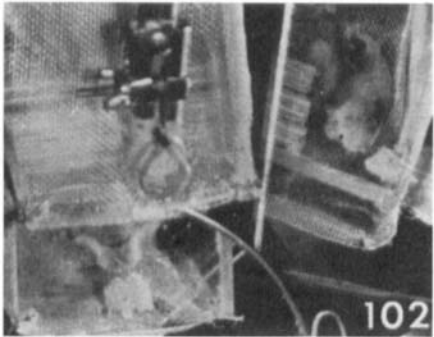
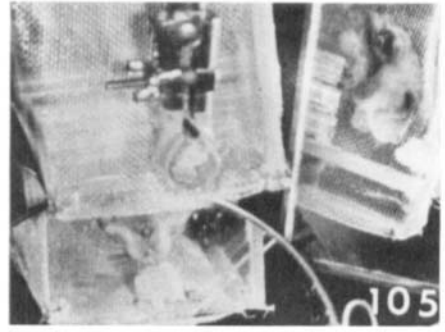
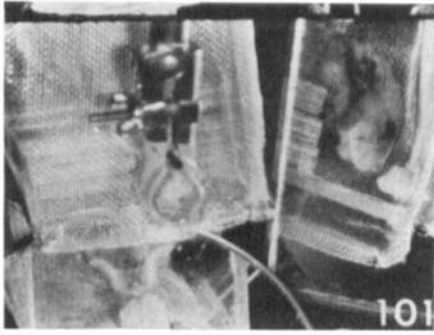


Figure 10

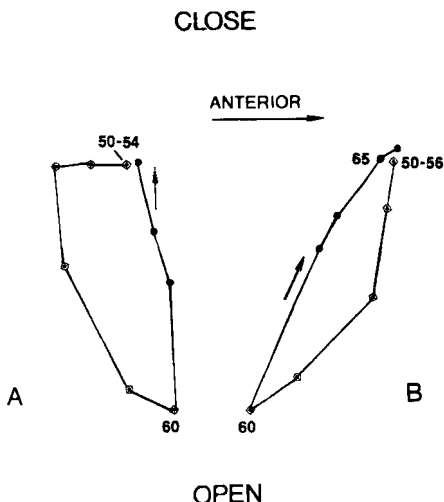


Fig. 11 *M. auratus*. Typical orbit of hamster chewing on pellet. Small arrows indicate the upstroke; in A, the arrow is on midline. Numbers correspond to the respective film frames.

A Frontal view showing transverse displacement. The upstroke is essentially on midline.

B Simultaneous lateral view showing the propalinal component of motion.

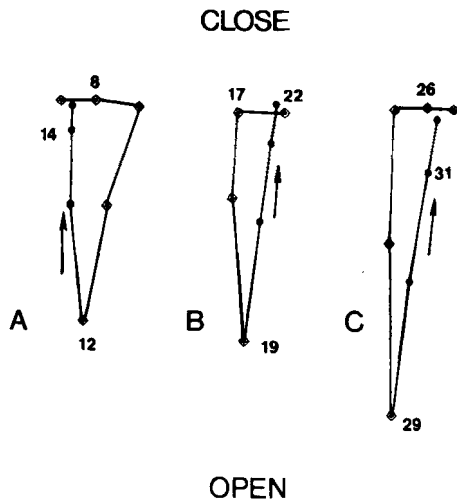


Fig. 13 *M. auratus*. Sequential frontal orbits of hamster chewing on pellet. The sequence proceeds in order from A to C. The arrows indicate the upstroke and midline; numbers correspond to film frames. These sequential orbits show typical variations in orbital path.

tion passes through zero (i.e., becomes a closing deceleration) and peaks, very abruptly in the case of seeds, but then diminishes towards zero as occlusion is approached.

Graphs of horizontal jaw displacement for seeds are regularly cyclic (fig. 14), whereas graphs for pellets (fig. 15) indicate irregular regions of small and large displacements. In both cases, the horizontal displacements of individual orbits exhibit the previously described pattern of lateral movements. In general, velocity and acceleration graphs for both foods peak in one direction near occlusion and then in the other during the downstroke. These peak amplitudes are somewhat greater for seeds; however, they are considerably less for both foods than are those of vertical.

Propalinal and vertical displacements (fig. 16) are mapped from a lateral cine view. The propalinal graphs show marked anteroposterior shifts accompanying the upstroke and downstroke. Graphs of vertical displacement, velocity, and acceleration closely resemble those derived from frontal views.

Fig. 14 *M. auratus*. Mastication of seed. Graphs of displacement, velocity, and acceleration plotted from a series of masticatory orbits, resolved into vertical and horizontal components for the mean movement at the tip of the mandible (as recorded at 38 fps.). The arrows indicate the direction of lateral and vertical movements. R, designates lateral translation to the right; L, to the left. Each orbit shows reversals in orbital direction. Note particularly the smooth transition from closing to opening on the vertical displacement curver and shifts in acceleration during the orbit.

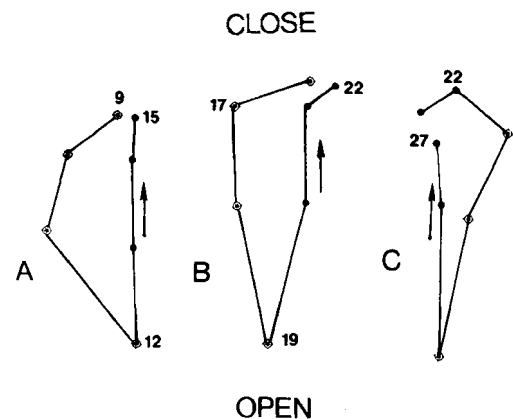


Fig. 12 *M. auratus*. Sequential orbits of mastication of a hamster chewing on a kernel of sunflower seed. The sequence proceeds in order from A to C. The small arrows indicate the upstroke and midline; numbers correspond to the respective film frames. Orbits B and C show reversal of orbital direction.

tions are generally three times peak opening accelerations. Both peak closing and opening accelerations are greater for seeds than for pellets. Opening accelerations peak near the bottom one-third of the downstroke and then decrease rapidly; closing acceleration peaks when the mandible changes direction. When the jaw is about half closed, closing accelera-

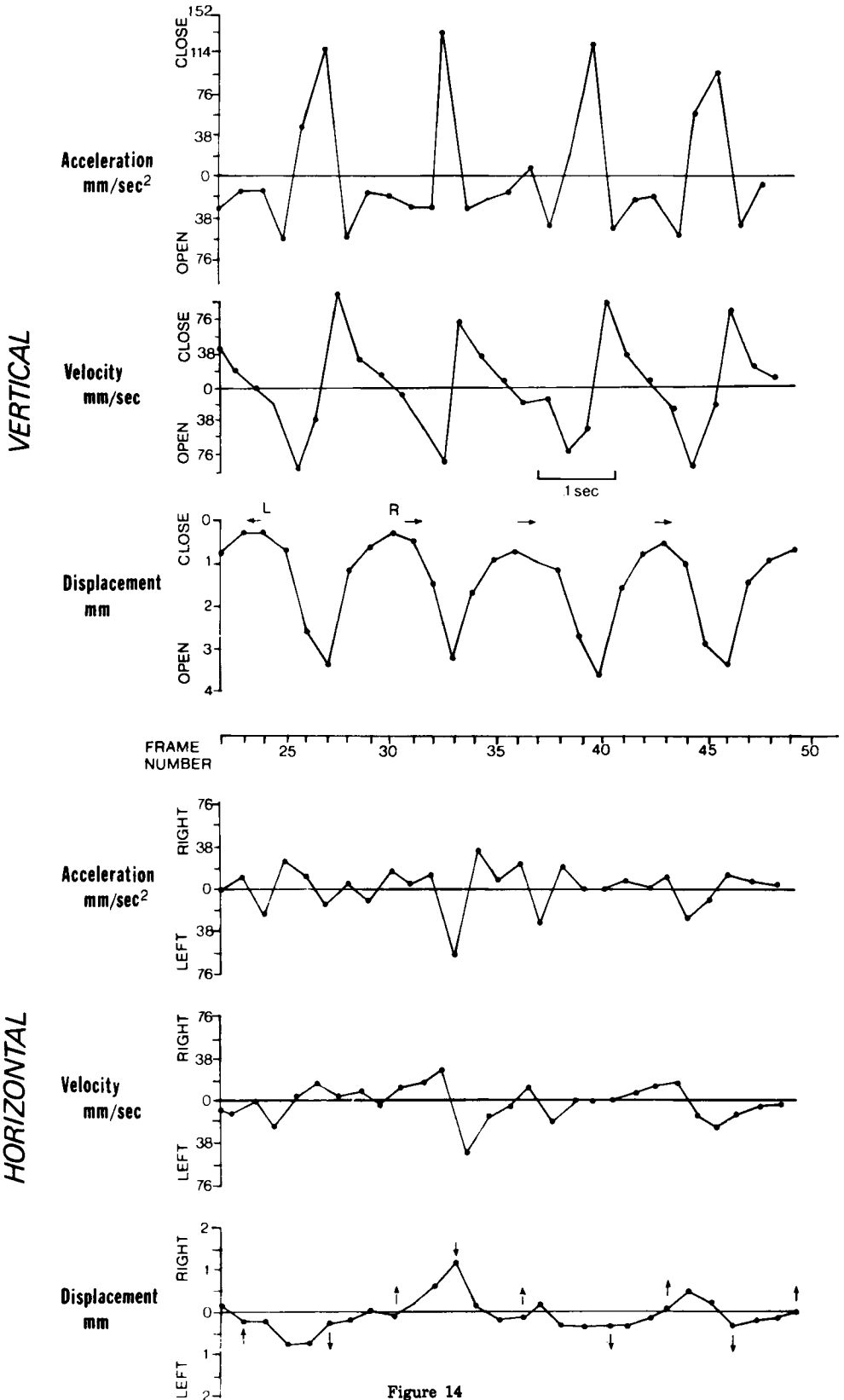


Figure 14

Propalinal acceleration graphs show that peak amplitudes in the anterior direction are generally twice those of peak posterior acceleration. Peak acceleration and velocity in the posterior direction correspond well with the sharp increase in posterior displacement during the lower half of the downstroke. Peak anterior acceleration is reached at the start of the upstroke as expected, as the teeth nearing occlusion will be affected by the energy the mandible then imparts to the food being reduced.

Electromyography

It is clear that hamsters have an active and passive side during chewing, though they may chew simultaneously on both sides about 10% of the time. This asymmetry was determined only after analyses of the data. However, to clarify the subsequent description of the electromyographic activity which accompanies jaw movements, I refer to the active side as ipsilateral and the passive side as contralateral. I also adopt the convention of describing only clockwise orbits in which the orbital direction and the passive side are on the right and the active side is on the left.

The major muscle groups are generally active symmetrically during the closing stroke of mastication. They fire asymmetrically during lateral translation when the mouth is closed and during opening. Electromyograms are correlated with masticatory movement during typical orbits, reversing as the orbital direction reverses (see fig. 17 for electromyographic sequences accompanying these reversals).

The lateral pterygoids typically fire asymmetrically (fig. 17A, for a right orbit; a left orbit shows a mirror image). With the mouth closed, the start of lateral movement (right) is accompanied by strong activity from the ipsilateral lateral pterygoid. Activity, if any, is very weak from the contralateral muscle. Near the end of this lateral translation, horizontal acceleration decreases concurrent with the initiation of strong firing from the contralateral lateral pterygoid; the amplitude from the ipsilateral muscle decreases (i.e., weaker than that on the right). Both lateral pterygoids are active at the start of the downstroke. However, as the jaw begins its return toward midline, (i.e., to the left) the contralateral muscle continues to fire strongly but activity ends from the ipsilateral pterygoid. The contralateral muscle stops firing about two-

thirds of the way through the opening stroke. During most of the upstroke, inconsistent low-level activities of both muscles are seen. Toward the end of closure, these muscles may stop firing, or when the orbit continues to the right, the ipsilateral lateral pterygoid may simply continue to fire, increasing in amplitude as lateral translation at the top of the orbit begins.

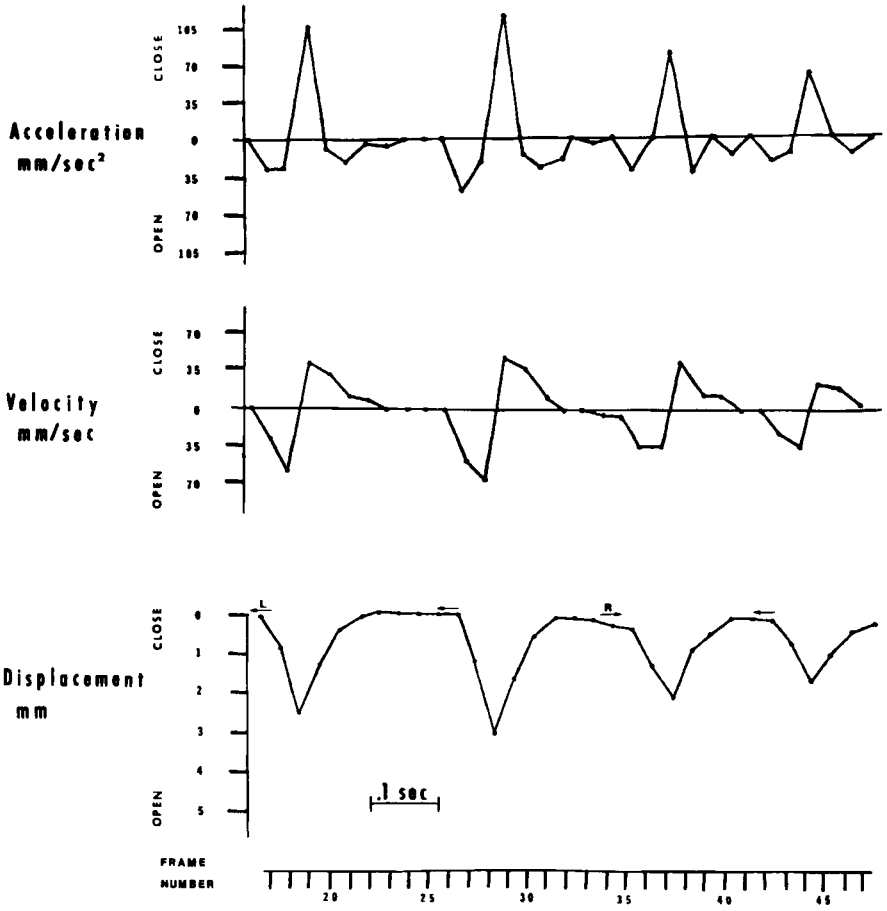
The anterior digastrics also act asymmetrically (figs. 17A,E). The ipsilateral anterior digastric starts to fire when the jaw begins to shift laterally at the top of the orbit. Both anterior digastrics fire in concert at the start of the downstroke. The contralateral anterior digastric then shows an increase in amplitude as lateral translation (left) returns to midline; the amplitude of the ipsilateral digastric remains unchanged. During the downstroke, the two anterior digastrics become inactive at nearly the same time, concurrent with the end of activity in the contralateral lateral pterygoid.

The posterior digastrics fire symmetrically and start later than their corresponding anterior digastrics. This lag in the start of posterior digastric activity between the ipsilateral anterior and posterior digastrics is more noticeable than between the contralateral muscles. The posterior digastrics become active at the start of the downstroke and stop firing simultaneously with the anterior digastrics.

The posterior and deep heads of the temporalis muscle on the same side fire nearly in concert (fig. 17B). Bilaterally, however, these muscles are active asymmetrically (fig. 17C). Lateral translation to the right at the start of the upstroke is accompanied by initial firing on the right side, although the left side becomes active shortly thereafter. The posterior and deep heads of the temporalis continue to fire bilaterally until the upstroke ends. Activities from the ipsilateral muscles then stop while the contralaterals continue to fire during lateral translation (right) at the top of the

Fig. 15 *M. auratus*. Mastication of pellet. Graphs of displacement, velocity, and acceleration plotted from a series of masticatory orbits, resolved into vertical and horizontal components for the mean movement at the tip of the mandible (as recorded at 35 fps.). The arrows indicate the direction of lateral and vertical movements. R, designates lateral translation to the right; L, to the left. The third and fourth orbits show reversals in orbital direction. In contrast to figure 14, notice the plateauing of the vertical displacement graph.

VERTICAL



HORIZONTAL

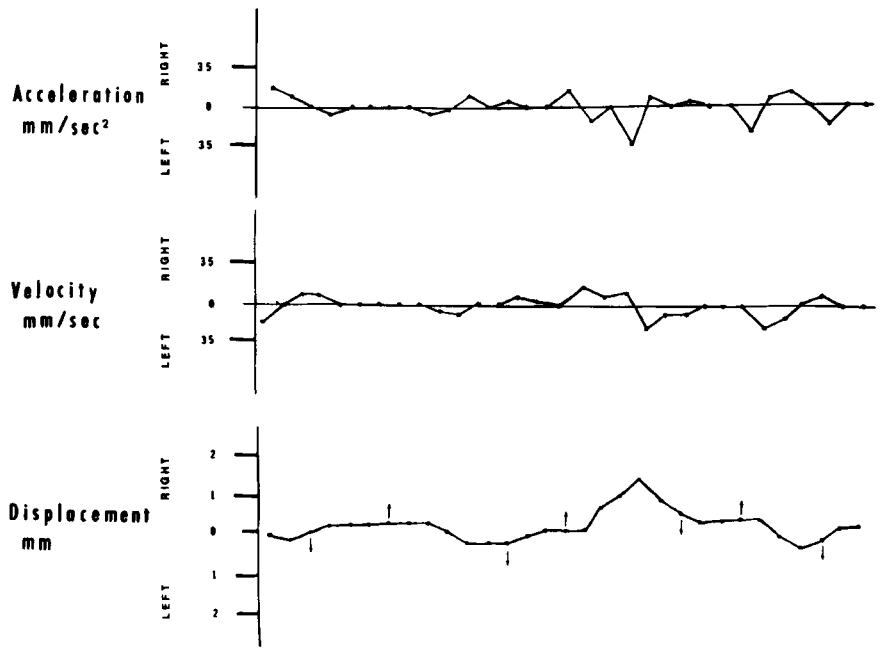


Figure 15

orbit. Contralateral heads stop firing as the jaw begins its downward motion.

The anterior temporales (fig. 17D) are usually active symmetrically. Only occasionally are they active asymmetrically, and then they fire in concert with asymmetric activity from their respective posterior temporalis. Symmetrical activities from the anterior temporales coincide with the upstroke and ordinarily continue into lateral translation at the top of the orbit. Both sides become silent when the downstroke begins.

The medial pterygoids (figs. 17E, 18A) begin to fire at the start of the upstroke. Firing is symmetrical when the upstroke proceeds along the midline. However, numerous records show asymmetric activity at the start of closing. A short lead in activity on the left side accompanies lateral translation to the right. During the rest of the upstroke, the muscles on both sides fire in concert. At the top of the orbit, continued activity from only the ipsilateral medial pterygoid accompanies lateral excursion to the right. Neither of the medial pterygoids is active during the downstroke.

The superficial masseters (fig. 17F,G) fire asymmetrically. The ipsilateral muscle begins to fire at the start of closing while the contralateral side starts at a low level a short time later. Although both muscles are active during the rest of the upstroke, the ipsilateral superficial masseter fires more strongly throughout the closing stroke even in those orbits which lack significant lateral translation. The ipsilateral muscle continues to fire strongly during lateral excursion at the top of the orbit, but contralateral superficial masseter activity ends.

The deep masseters (fig. 17D,G) begin to fire at the start of the closing stroke. Firing is symmetrical during the upstroke and into lateral translation at the top of the orbit, regardless of orbital direction. Consequently, the ipsilateral superficial and deep masseters fire in concert (fig. 17G), but activity from the contralateral deep masseter starts earlier and ends later than that of the contralateral superficial masseter. Both deep and superficial masseters are silent during the downstroke.

The few electromyograms available from the anterior zygomaticomandibularis muscle show that it fires at the same time as the deep masseter.

In chewing orbits without marked lateral translation, bilateral records are generally symmetrical. Adductor muscles fire only dur-

ing the upstroke and the digastrics only during the downstroke, but the lateral pterygoids are active during both strokes. Only the superficial masseters fire asymmetrically. The superficial masseter on one side still shows stronger relative amplitudes during the upstroke. In contrast, the deep masseters and apparently zygomaticomandibulares fire symmetrically.

Some electromyograms from animals during gnawing are available (fig. 18). Gnawing behavior involved a scraping or chipping motion of the lower incisors. The adductor muscles are noticeably less active when these animals are gnawing, whereas the anterior and posterior digastrics as well as the lateral pterygoids fire more strongly and for longer periods of time. Electromyograms are also available from the temporalis, masseter and medial pterygoid muscles when hamsters are biting kernels of sunflower seeds. These records suggest that the adductors fire strongly (as during chewing) when hamsters bite.

DISCUSSION

Feeding behavior

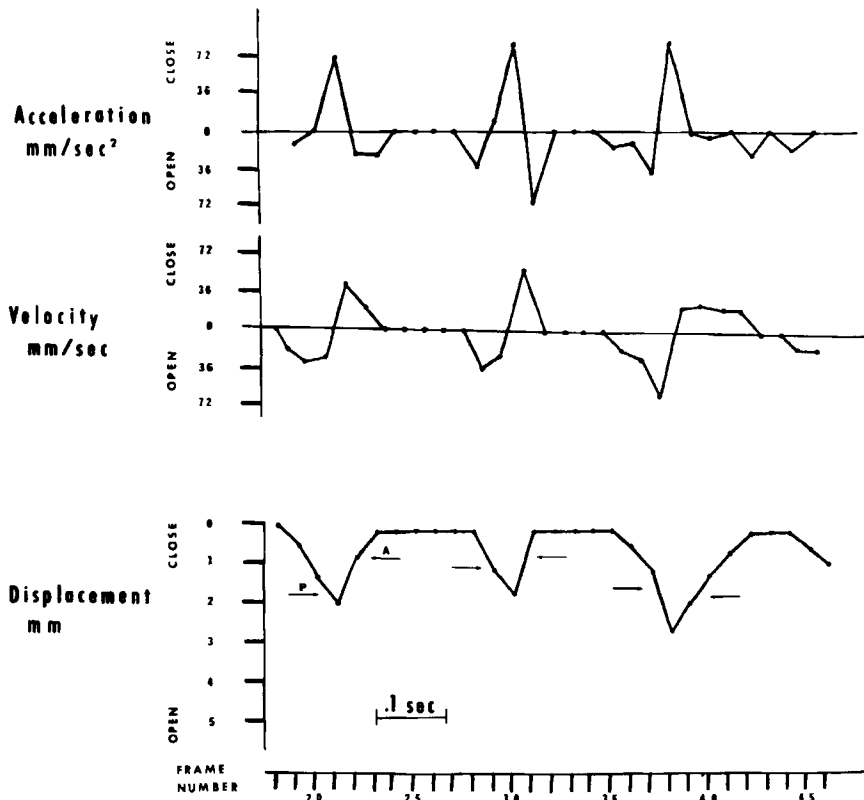
Rodents chew in distinct ways (cf. Woods, '76; for the patterns used by hystricomorphine rodents). In rats (Weijs, '75) and "textbook" rodents (Peyer, '68; Turnbull, '70), only a simple anteroposterior motion accompanies opening and closing. However, hamsters exhibit a marked lateral movement, coupled with this strong propalinal translation.

The interlocking molar cusps of hamsters restrict protrusive, retrusive and true transverse movements. Manipulations show that a twisting movement in the horizontal plane will unlock this occlusion. Thus, lateral translation observed at the top of the orbit apparently results from rotation of the mandible about a vertical axis, possibly through the condyle (cf. de Vree and Gans, '76, for goat). The inward slant and roomy mediolateral extent of the mandibular fossae suggest that such rotation must be accompanied by a protrusive and medial condylar movement on the opposite side.

Lateral translation observed at the top of

Fig. 16 *M. auratus*. Mastication of pellet. Graphs of displacement, velocity, and acceleration plotted from a series of masticatory orbits, resolved into vertical and propalinal components for the mean movement at the tip of the mandible (as recorded at 36 fps.). The arrows indicate the direction of anteroposterior and vertical movement. P, posterior; A, anterior; O, open; C, close.

VERTICAL



PROPAGINAL

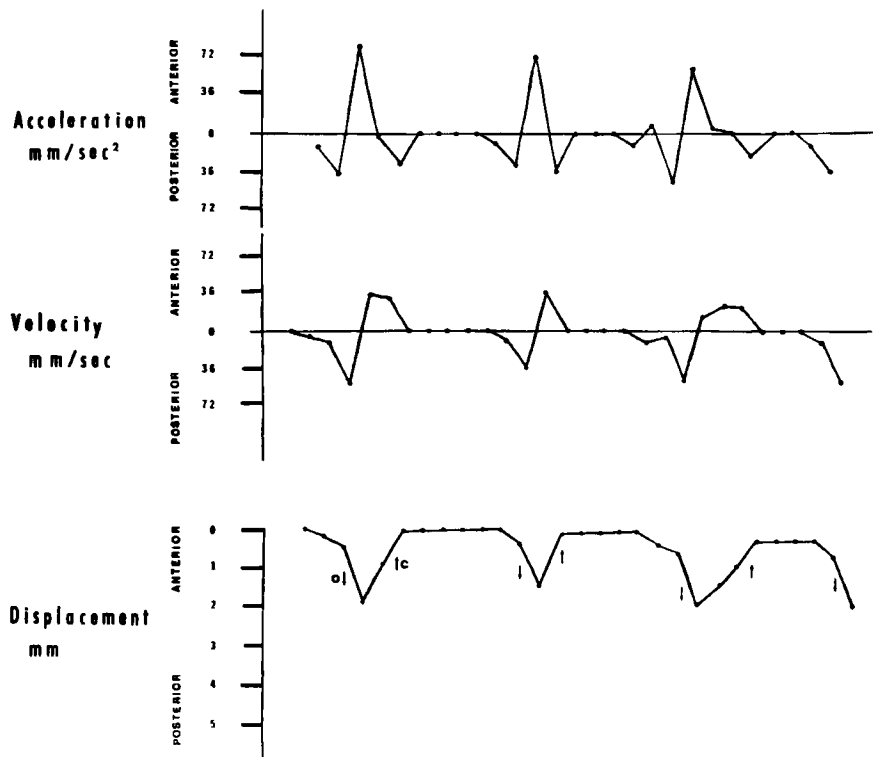


Figure 16

the orbit merits emphasis. First, when the molars are near occlusion, the lower incisors, which are parallel and slightly posterior to the upper incisors, cross the midline. This incisal position would restrict the kind of protrusive movement described in albino rats (Weijs, '75) as the incisors would be brought into contact. However, the position of the incisors permits rotation of the mandible about a vertical axis or a nearly straight vertical opening movement along the midline. When comparison is made to a vertical scissor-like motion, rotation about a vertical axis imposes additional shearing forces upon the food. Thus, lateral translation appears to increase trituration. Secondly, hamsters store food in their cheek pouches. Lateral movements may be advantageous during this process as buccal movements of the teeth might assist them in maneuvering food towards a cheek pouch. Furthermore, lingual movements may help return food from the pouch to the oral cavity. Hamsters can also pouch impressively large foods. However, a midline position of the lower incisors partially blocks the entry of large solid food objects, such as whole pellets. A lateral shift of these teeth would enlarge this entrance, permitting larger food items to be stored. With small foods, such as sunflower seeds, a lateral incisal movement appears to be less advantageous during pouching. But, a rapid lateral thrust produced by these teeth may help propel small food items from between the incisors towards a cheek pouch.

When lateral rotation at the top of the orbit ends to the right of midline, the left condyle is protruded with respect to the right. During the subsequent downstroke the mandible returns to midline, suggesting that the right condyle moves forward for a greater distance than the left. However, at the start of the downstroke, the tip of the jaw shows only slight posterior and lateral movement, which suggests that the condyles are initially rotated about a transverse condylar axis in order to clear the incisors. The mandible then moves toward midline and posteriorly, which increases the vertical distance between the molars and permits food to be placed more readily between the teeth. Therefore, condylar movements during the downstroke appear to involve an initial bilateral rotation about a transverse axis, which is then followed by marked bilateral but asymmetric condylar protrusion. Examination of the temporomandibular joint suggests that these gross move-

ments involve (1) an anteroposterior sliding movement between the articular disc and the mandibular fossa, and (2) a rotational motion about a transverse axis between the mandibular condyle and the articular disc.

The upstroke in hamsters tends to be on midline. Lateral movements at the start

Fig. 17 *M. auratus*. Representative electromyograms recorded during chewing. Each record shows simultaneous activity from four muscles. All traces proceed in time from left to right. One-second markers (T) indicate the time base for all traces. The first letter of each muscle label indicates it is right (R) or left (L). Frame markers (FRM) allowed correlation between masticatory events and electromyographic activities. Orbital direction refers to the direction of lateral translation at the top of the orbit.

A Activities from both anterior digastrics (AD) and lateral pterygoids (Lpt). The sequence begins with right orbital direction. The arrows, here and elsewhere, indicate reversals in orbital direction disclosed by simultaneous cinematography. All four muscles are active at the start of opening. The slight lead shown by the right lateral pterygoid at the end of the first burst of firing accompanies lateral translation to the left during the downstroke.

B Activities from the deep masseter (DM), and anterior (AT) posterior (PT) and deep (DT) heads of the temporalis on the same side. The posterior and deep heads of the temporalis essentially fire symmetrically. The anterior head, however, fires more nearly in concert with the deep masseter.

C Activities from both posterior temporales (PT), unilateral deep masseter (DM) and medial pterygoid (Mpt). The posterior temporales usually fire asymmetrically. The lead shown by these closing retrusors accompanies lateral excursion to that side. Symmetric activities from the deep masseter and posterior temporalis of the same side produce a rotational force couple which swings the mandible upward. The reduced activities shown for the medial pterygoid result from insufficient signal amplification as numerous other electromyographic traces of this muscle exhibit amplitudes comparable to those seen in other closing muscles.

D Activities from bilateral deep masseters (DM) and anterior temporales (AT). Deep masseter activities are symmetrical. Symmetric activities from the deep masseters and anterior temporales produce a unilateral force couple on both sides during closure.

E Activities from both medial pterygoids (Mpt) and anterior digastrics (AD). This record shows medial pterygoid activities to be symmetrical, although numerous records also show asymmetric activities accompanying lateral translation. Bilateral anterior digastric activities show asymmetry. The leads shown by these opening retrusors correspond to transverse movement across the top of the orbit.

F Activities from anterior (AT) and posterior (PT) temporales on the same side and both superficial masseters (SM). Stronger firing amplitudes shown from the temporalis and opposite superficial masseter (first arrow) accompany orbital direction to the right, a bilateral force couple.

G Activities from the superficial (SM) and deep (DM) masseters, medial pterygoid (Mpt) and anterior digastric (AD) all of the same side. Stronger amplitudes shown from the superficial masseter and medial pterygoid accompany orbits to the right. Deep masseter activities display a consistent amplitude regardless of orbital direction.

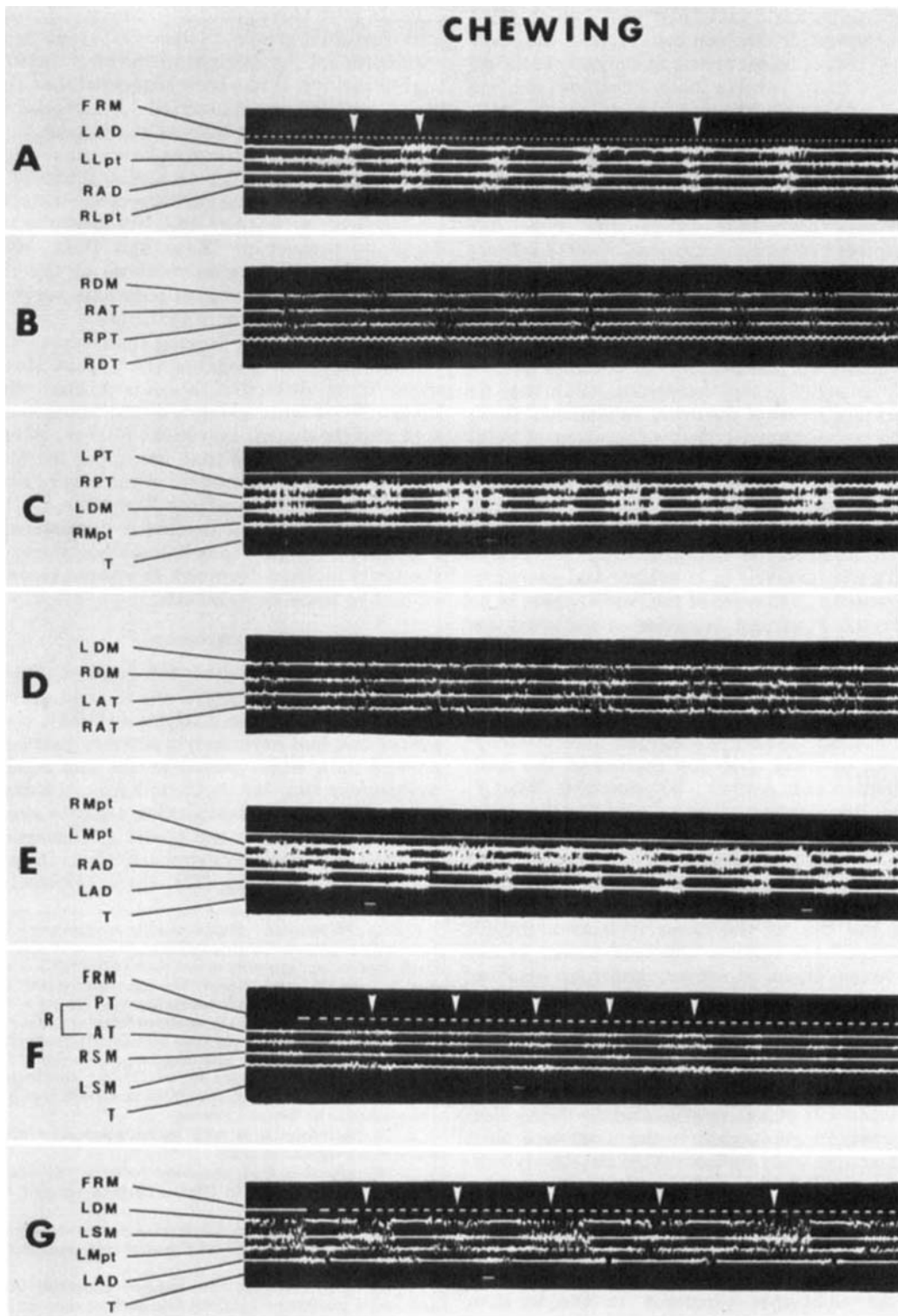


Figure 17

apparently are final adjustments which align the isognathic teeth on both sides of the jaws. Food reduction occurring at the end of the upstroke may involve both crushing of food wedged between the molar cusps (compression forces) and shearing forces generated as the lower molars move forward during closure.

Different food types affect the chewing pattern. Graphs of displacement resolved in vertical and horizontal components show differences between mastication of soft sunflower seed kernels and hard laboratory pellets. The most noticeable difference is observed when the mouth is closed. Consequently, foods of different textures apparently have a greater effect on masticatory movements during the period of actual trituration than they do during the rest of the orbit. In addition, these differences suggest that trituration of relatively soft foods involves primarily shearing forces, and hard foods are broken down by a combination of compressive and shearing forces.

Different foods also affect the movement patterns involved in pouching and gnawing. In pouching, the size of the food appears to be critical. Pouching behavior is different for large pellets than for small sunflower seeds. These changes in the movement pattern involve the degree of mouth opening, use of the forepaw and incisors, and the amount of head movement. As for gnawing, jaw movement appears to differ with the texture of the food. Hiimeae and Ardran ('68) describe "biting" and "true gnawing" in rats as two separate processes, depending upon the food type. Thus, it might be preferable to differentiate between biting and gnawing among rodents. Biting involves a straight closure of the mouth. As the tips of the lower incisors approach those of the uppers, the food object is cut between them. However, gnawing involves scraping or chipping movements of the lower incisors along food objects stabilized by the uppers. Both processes would appear beneficial in rodents with omnivorous diets, such as hamsters and rats. Biting movements may be used on soft plant material and the fleshy food of a vertebrate carcass. In the latter case, both upper and lower incisors could cut deeply into the meat, which could then be torn away by head and body movements. A gnawing motion may be more useful for shaving hard, solid plant material and scraping remnants of meat from bones.

An additional comment on the incisors seems appropriate here. The incisors of

rodents grow throughout life (Peyer, '68), and this continual growth requires constant wear (and constant sharpening) in order for the animal to survive. It has been suggested that the lower incisors are sharpened by movements across the labial surfaces of the uppers, and that the uppers are sharpened by normal wear during ingestion (Hiimeae and Ardran, '68). In hamsters, the labial surfaces of the incisors are covered by enamel and the lingual surfaces by cementum (Keys and Dale, '44). Hence, only the lingual surfaces of the incisors wear. Condylar manipulations suggest that the lingual surfaces of the lower incisors may be sharpened by moving them across the enamel surfaces (labial) of the uppers. However, it is difficult to believe that the hollowed-out wear pattern of the upper incisors results during ingestion. Rather, it appears more plausible that the upper incisors are sharpened by movement of the lower teeth across their lingual surfaces. Therefore, tooth-sharpening seems to involve a consistently changing labial and then lingual movement of the lower incisors. However, it was not recorded during these experiments.

Electromyography

Electromyograms recorded from masticatory muscles of hamsters are in good agreement with the motion analysis and show both symmetric and asymmetric activity patterns as well as a silent period at the end of the downstroke (fig. 19). Activities from the deep masseters, anterior temporales, anterior zygomaticomandibulares and posterior digastrics are usually bilaterally symmetrical. As in rats (Weijs and Dantuma, '75), these symmetric

Fig. 18 *M. auratus*. Representative electromyograms recorded during first chewing and then gnawing of a pellet. Each chewing and gnawing record shows simultaneous activities from the same animal. The top three records are continuous; the bottom one was recorded on the same day but in different sessions at the same amplification. One-second markers (T) indicate the time base for all traces. The first letter of each muscle label designates it as right (r) or left (l). Frame markers are shown (FRM). Electromyographic records A, B, C, show reduced amplitude from the adductor muscles during gnawing.

A Activities from both medial pterygoids (Mpt) and anterior digastrics (AD).

B Activities from unilateral posterior temporalis (PT) and medial pterygoid (Mpt) and both anterior digastrics (AD).

C Activities from bilateral anterior digastrics (AD) and unilateral superficial masseter (SM) and lateral pterygoid (Lpt).

D Activities from both anterior digastrics (AD) and lateral pterygoids (Lpt). All four muscles show an increase in duration of activity during gnawing.

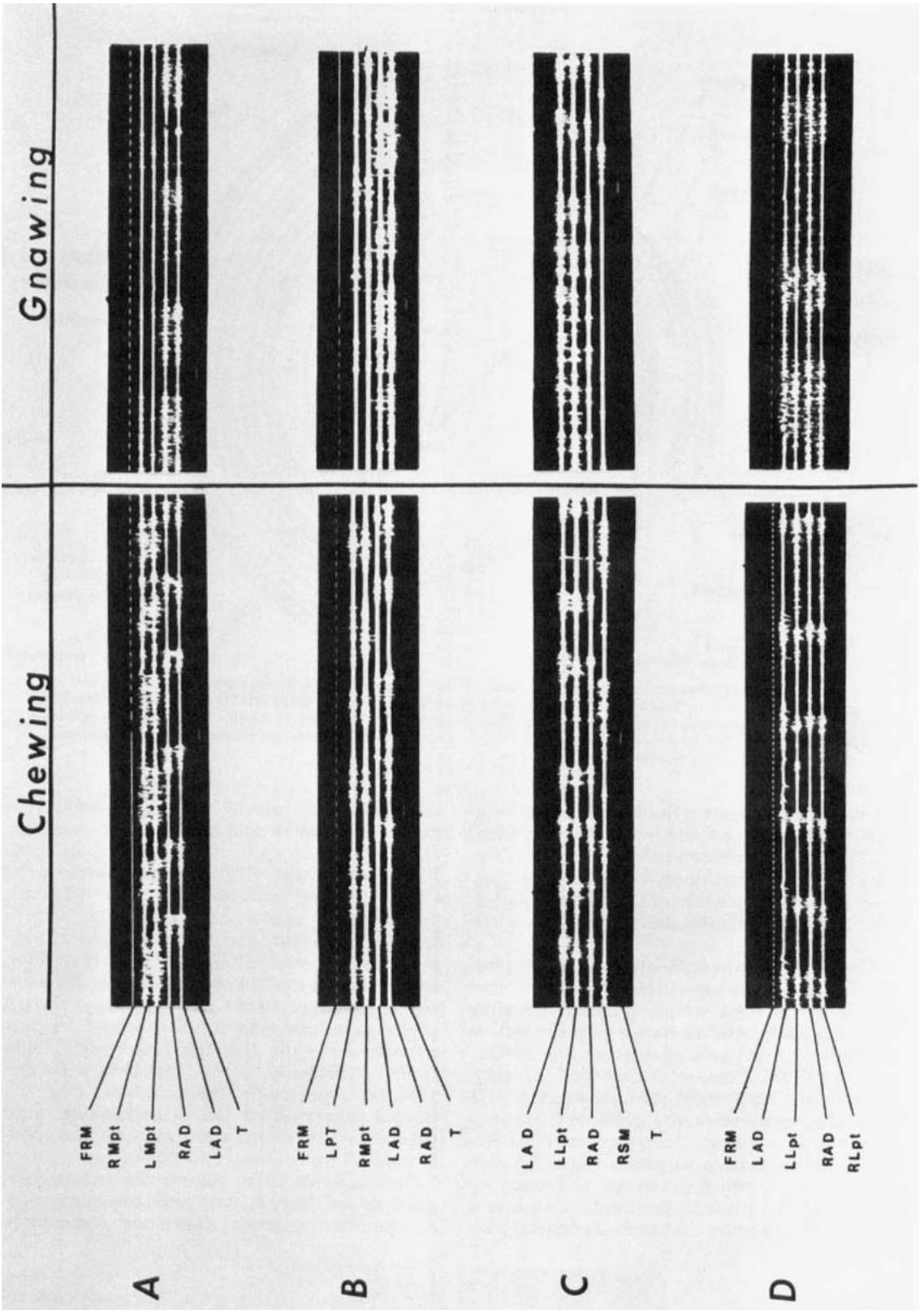


Figure 18

FRONTAL VIEW

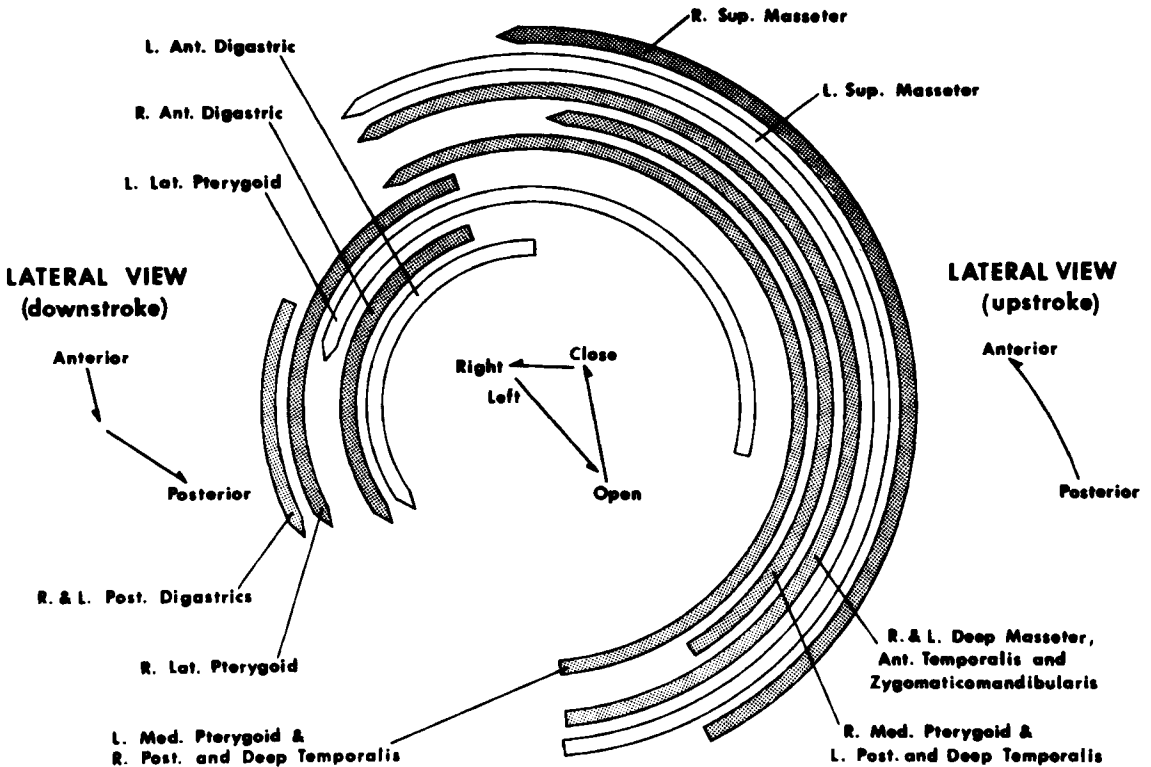


Fig. 19 Diagram summarizing a typical sequence of jaw muscle activities for continuing masticatory orbits in the same direction. In frontal view (center), lateral translation at the top of the orbit is right; the downstroke shows a lateral component of motion to the left. The upstroke begins to the left of midline but then proceeds initially to the right to close on midline. In lateral view, propalinal movements are shown during the upstroke (viewers right) and the downstroke (viewers left).

activities tend to move the jaw along the midline. However, the other muscles studied usually fire asymmetrically during a typical chewing orbit. Asymmetric activities accompany lateral movements at the top of the orbit, during the downstroke, and at the start of the upstroke.

Electromyograms indicate that the lateral translation at the top of the orbit is produced by a bilateral force couple which pits closing retrusors (deep and posterior temporales) on the contralateral side against closing protrusors (superficial masseter and medial pterygoid) on the ipsilateral side. In concert with these closing muscles, the ipsilateral anterior digastric and lateral pterygoid muscles fire before the contralateral, producing a unilateral force couple which accompanies lateral excursion to the contralateral side. One might expect, for example, that activity from the ip-

silateral (left) lateral pterygoid would produce a protrusive and medial force, rotating the jaw to the right (as described in bats, Kallen and Gans, '72); retrusive forces generated by the ipsilateral anterior digastric would appear to counteract this condylar protrusion. However, the anterior digastric inserts on the ventral limit of the mandible, which is well medial of the condyle. As a result, a medial retrusive force applied at the tip of the mandible may rotate it about an axis passing vertically through the condyle. This condylar rotation, acting together with the protrusive and medial forces induced from the lateral pterygoid on the same condyle, may then generate lateral translations in the opposite direction.

As the downstroke begins, the anterior digastrics and lateral pterygoids are bilaterally active. The anterior digastrics apparently

generate a retrusive force ventral to the condyles and the lateral pterygoids a protrusive force at the condyles. Together, these forces allow the incisors to clear by a rotation of the mandible about a transverse axis, which passes through both condyles. As opening proceeds, activity ends initially in the ipsilateral lateral pterygoid; the contralateral lateral pterygoid continues to fire. This continued activity from the contralateral side apparently generates an unbalanced protrusive force on that side returning the mandible to midline. Thus, it appears that the jaw is translated laterally during the downstroke by unilateral activity from the lateral pterygoid and that the mouth is opened by the pull of the digastrics, acting ventral to the instant center of rotation.

Even though the jaws move in a downward and posterior direction through the bottom one-fourth of the opening stroke, all the obvious masticatory muscles studied are silent. It might be possible that this motion is a product of momentum and gravity. However, in rats (Weijs and Dantuma, '75), miniature pigs (Herring and Scapino, '73), and Virginian opossums (Crompton et al., '77), the suprahyoid muscles are very active at the end of opening. These muscles may also help to generate the final phase of the opening movement in hamsters.

In hamsters, the upstroke is along the midline with all the adductor muscles taking part in this motion. A unilateral force couple on both sides is produced by closing protrusors, which act vertical to the condyle, and closing retrusors acting dorsal to it. This combination moves the mandibular tip dorsally along midline as in rats (Weijs and Dantuma, '75). As the jaw is moved laterally at the top of the orbit, bilaterally symmetric activities from the deep masseters and anterior temporales continue to produce a closing force. This force is apparently responsible for maintaining the teeth in contact with the food and continuing efficient reduction.

Therefore, chewing in hamsters involves a lateral translation superimposed over a simple rotational force couple. Lateral movements are generated by asymmetric activities, generally pitting protrusors on one side against retrusors on the opposite side. Symmetric vertical protrusive and dorsal retrusive forces from the adductors then produce a pair of unilateral force couples, which rotate the jaw on midline during the upstroke.

During gnawing, electromyographic activities show a marked reduction in activity of closing protrusors and retrusors. This reduction of adductor activity differs from that described in rats during biting (Weijs and Dantuma, '75). Thus, it appears that biting and gnawing are two mechanically different processes at least among rodents, and that the scraping and chipping movements during gnawing require less of a closing force than those of a bite.

Trituration

Most studies on mammalian mastication refer to an active chewing side (Ardran et al., '58; Becht, '53; Crompton and Hiimae, '68; de Vree and Gans, '76; Kallen and Gans, '72; Smith and Savage, '59). However, the presence and/or absence of an active side is still an open question for animals with isognathic dentitions, such as hamsters. Hiimae and Ardran ('68) note that rats had food simultaneously between the molars of both sides as well as on one side only, suggesting to them that rats occasionally exhibit an active side while chewing otherwise occurs bilaterally. On the other hand, Weijs ('75) only noted a bilateral reduction of food in rats. Herring and Scapino ('73) report that electromyography of the masseter suggests a "dominant side" in miniature pigs and note that this dominance is not necessarily an indicator of an active side. They suggest that chewing may be bilateral and involve a more efficient breakdown of food on one side than the other. However, their results are uncertain because they were unable to tell at any instant the side on which the animal was chewing.

The present study suggests that hamsters have an active chewing side. Even though the main axis of the closing stroke is vertical as in cats, cats definitely reduce food on only one side at a time (Gorniak, '77). Thus, a midline closing stroke does not necessarily mean that the animal chews bilaterally.

Although hamsters have the potential for bilateral food reduction, this process would not appear to be for very efficient. Lateral excursion at the top of the orbit always moves the mandibular molars buccally on one side and lingually on the opposite side. If reduction were to occur bilaterally, food lying on the side of buccal movement would then be pushed towards a cheek pouch. While this food might be pouched, cine films show no indication that hamsters store food between chewing orbits.

It would seem that an active chewing side might be more efficient, but only if it was on the side in which the molars move lingually at the top of the stroke. Most triturated food may then be deposited directly into the oral cavity, decreasing the time and energy otherwise needed to retrieve food pushed buccally between the teeth and cheek pouch.

Data suggest not only that hamsters have an active and passive side, but also that an active side might be typical of trituration. In orbits with and without significant lateral translation, the superficial masseter muscle consistently fires more strongly on one side than the other during midline closure. As food resists closing, this strong activity from the superficial masseter suggests that trituration in hamsters is concentrated on that side. Furthermore, the majority of orbits observed in hamsters show lateral translation. Similar lateral components of motion occur in bats (Kallen and Gans, '72), rabbits (Ardran et al., '58) and ungulates (Beckt, '57; de Vree and Gans, '76; Smith and Savage, '59). In all these species, lateral excursion at the top of the orbit proceeds from the active to the passive side. This excursion pattern suggests that hamsters typically have an active side which is opposite the direction of lateral translation at the top of the orbit and during which food is deposited into the oral cavity by lingual movement of the mandibular molars and strong activity recorded from the superficial masseter.

Control of mastication

It was not the purpose of this study to examine the nervous control of mastication. However, the results permit comments regarding several aspects of nervous activity.

1. Sherrington ('17) and Kawamura et al. ('60) documented reciprocal inhibition between antagonistic muscles for opening versus closing activity, a concept that also applies to the mastication of hamsters. Kallen and Gans ('72, in little brown bats) extended the concept of reciprocal inhibition to include lateral translation during chewing. The present study provides additional evidence in support of this latter concept.

In hamsters, lateral translation across the top of the orbit starts with the tip of the mandible on midline. Although the respective muscles on both sides would be stretched equally in this starting position, asymmetric activities from protrusors on one side and retrusors on the other accompany this lateral

excursion. Sherrington's classical study showed that stimulation of the periodontal structures produces rapid mouth opening, followed immediately by closing; the antagonistic muscles reciprocally inhibited. Consequently, lateral translation across the top of the orbit may involve reciprocal inhibition, triggered by pressure on the periodontal structures as the teeth contact the food. Differential outputs from periodontal receptors may explain the differences observed in masticatory movement at the top of the orbit when a particular animal chews foods varying in consistency (de Vree and Gans, '76).

2. Masticatory orbits of hamsters reverse after one to three cycles. These reversals may relate to the jaw-opening reflex, which can be triggered by stimulation of the periodontal structures (Sherrington, '17; Hannam and Matthews, '69) and influenced by higher cortical levels (Kawamura, '67; Chase and McGinty, '70). Thus, changes in pressures on the periodontal structures, produced by changes in vertical resistance to food, might be integrated at higher nervous levels and might contribute to triggering of a reversal in orbital direction. The same concept may be used to explain changes observed in masticatory movement when the same animal chews different food types (de Vree and Gans, '76). Foods of hard consistency, such as pellets, probably produce more resistance to breakdown than the softer kernel and would tend to generate greater pressure on the periodontal structures during trituration. In turn, this periodontal input may facilitate responses at a higher cortical level to maintain tooth-to-food contact, explaining the nearly horizontal path followed by the mandible at the top of the orbit. On the other hand, the softer kernel would offer less resistance and induces less pressure on the periodontal structures. The absence of closing signals may allow the mouth to open slightly, as observed during lateral translation.

3. Karamura et al. ('67) suggest that mechanoreceptors in the temporomandibular joint regulate biting strength. Kallen and Gans ('72) further suggests that these receptors serve an important protective function. Because the mandibular fossae of hamsters are free of anterior and posterior bony limits, this latter suggestion leads to the prediction that the mechanoreceptors of rodents must be highly concentrated along the anterior and posterior limits of the joint. Furthermore, an anterior concentration of receptors might also regulate

the maximum size of food hamsters are capable of storing in their cheek pouches.

4. The length of the incisors in rodents must be continually monitored in order to adjust sharpening rate to compensate for growth minus wear. X-rays and prepared specimens of hamsters show that the lower incisors nearly abut the floor of the palate when the mouth is fully closed. Possibly, both lingual and palatal touch receptors monitor such length and influence the sharpening pattern.

Comparison

Hamsters chew differently than rats. Both rodents may utilize the same food types, and both have essentially the same general muscular configuration as well as a characteristic temporomandibular joint. However, the occlusal surfaces of the molars are very different in these two myomorph rodents (figs. 3, 4), and each reflects a particular masticatory movement. Thus, as suggested by Kallen and Gans ('72), the occlusal pattern of the dentition has a greater influence on that aspect of masticatory movement when reduction takes place than do the corresponding muscles, joints, or bony elements which are often used to define chewing motion.

Both rats (Weijs and Dantruma, '75) and hamsters show symmetric muscular activities accompanying symmetrical movements of both sides of the mandible during closing. In hamsters and bats (Kallen and Gans, '72), asymmetric muscular activities occur during the clearly asymmetric lateral translation. However, asymmetric activity from the superficial masseter of hamsters demonstrates that asymmetric activity may be seen accompanying a seemingly symmetric motion. Furthermore, it emphasizes that the resistance against which an element is traveling should be considered. For instance, although carnivores are purported to exhibit a scissors-like masticatory movement (Smith and Savage, '59; Turnbull, '70), asymmetric muscle activity might be observed during closing when the vertical resistance imparted by the food is much greater between the carnassials of one side than those of the other (such as dogs chewing on bones).

In contrast to rats (Weijs and Dantuma, '75) and little brown bats (Kallen and Gans, '72), the anterior and posterior digastrics of hamsters do not fire in concert. The connective tissues between the origin of the anterior and the insertion of the posterior digastrics

attach directly to the hyoid apparatus. Consequently, the anterior digastrics are mechanically capable of moving the mandible, independent of the posterior digastrics.

Hiiemae and Ardran ('68) describe both an active side and bilateral chewing in rats, whereas Weijs and Dantuma ('75) refer only to bilateral chewing. However, the latter authors did mention that they observed some asymmetric activity, but these were not analysed. Furthermore, they show electromyograms from the superficial masseters which resemble those recorded from the same muscle in hamsters. Perhaps such asymmetric activities are in the nature of a fine control mechanism which maintains a vertical chewing stroke when the consistency or amount of food differs between the left and right toothrows. This activity may, in fact, support the suggestion of Hiiemae and Ardran ('68) that rats chew occasionally on only one side (active side).

Of the literature available on mammalian mastication, only a small proportion involves the reduction of foods of varying consistencies (de Vree and Gans, '76; Luschei and Goodwin, '74). These studies and the present one show that a noticeable change in the chewing orbit occurs with different foods when the jaws are in closest approximation.

This study then confirms that rodents use different masticatory orbits, even when their diets and anatomy are superficially similar. Some species may exhibit strong propalinal movements without significant lateral translation. However, other species, such as hamsters, may show a prominent lateral component of motion upon essentially the same, strong propalinal movement. Furthermore, the present study notes the possible advantage of lateral translatory movement in an animal which stores food in cheek pouches. Additional studies, specifically on pouching and mastication in other animals which pouch foods, such as squirrels or old world monkeys, should increase our outer base of information for drawing conclusions regarding the evolutionary development of mammalian mastication systems.

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