

The functional significance of the position of the centre of rotation for jaw opening and closing in the rabbit

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INTRODUCTION

The mandible opens and closes by rotation about a transverse horizontal axis. In most mammals the mandibular condyles show a marked capability of antero-posterior displacement, made possible by highly incongruent joint surfaces. Lateral excursions of the jaw can be effected by protrusion of one condyle. But in man (see Brown, 1975, for review) and in most mammals (see Hiimeae, 1978, for review) jaw opening is also combined with such condylar displacement occurring bilaterally. The opening-closing movement can therefore be described as a rotation about a transverse axis, situated somewhere between the condyles and jaw angle. In man, the axis is usually located 2.5–4 cm below the condyles and somewhat behind them (Brown, 1975).

The following four hypotheses have been offered to explain the functional significance of the position of the centre of rotation (CR) for mandibular opening and closing so far below the condyle. (1) Stretching is avoided of the mandibular nerve, that enters the mandible about halfway up the ramus (Moss, 1959). (2) Compression is avoided of soft tissues, primarily the parotid gland, retromandibular blood vessels and facial nerve, between the posterior border of the ramus and the mastoid region of the skull (DuBrul, 1980). (3) Length changes of the fibres of the jaw-closing muscles are avoided, so that these muscles can, at a variety of gapes, act near optimum length (Carlson, 1977). (4) The leverage and hence the mechanical advantage of the jaw-closing muscles is increased because the CR is further away from the working lines of the muscles than the condyle (Grant, 1973). However, this argument has been shown to be based on misapplication of statics (Stern, 1974).

The purpose of this paper is to investigate the functional explanations for the CR position in the rabbit. This animal has a very long ascending ramus and a more or less upright body position, making it a suitable model to study jaw opening and closing movements. The location of the centre of mandibular rotation was measured by cineradiographic recording of natural jaw movements. Possible variation in location was studied in two ways. Firstly, because it is known (Weijs & Dantuma, 1981) that maximum gape and jaw opening and closing speed are dependent on the consistency and shape of food particles masticated, the effect of the kind of food upon CR location was investigated. Secondly, there is a difference in skull shape, muscle lines of action and muscle fibre length between newly weaned and adult animals (Weijs, Brugman & Klok, 1987). As these differences affect the length changes imposed on the jaw muscles, the position of the CR was studied in these two age groups.

To test the first two hypotheses mentioned above the effect of rotation patterns on retromandibular tissue compression and the stretching of cranial nerves was investigated. To test the third hypothesis a computer model was devised to describe the

length changes of the jaw muscle fibres as a function of the degree of jaw opening (Weijs *et al.* 1987). With the help of earlier sarcomere length measurements (Weijs & van der Wielen-Drent, 1982, 1983) and data from the literature (Muhl, Grimm & Glick, 1978) the maximum active forces at different degrees of opening could be predicted. The CR was thereby altered in a vertical plane. Since passive elastic forces might play a role in resisting jaw opening a (fifth) hypothesis was formulated, stating that the position of the CR is such that passive muscle forces are avoided. To test it, the elastic behaviour of muscle fibres was incorporated in the model. The parameters describing the length-force relationship were estimated from measurements of total passive resistance of the system against opening at different gapes in postmortem experiments.

MATERIALS AND METHODS

Materials

Male New Zealand domestic rabbits (*Oryctolagus cuniculus L.*) in two age groups were used for all experiments. The ages were 3–4 weeks (newly weaned) and 3–5 months (adults). The young animals weighed 300–500 g, the adults 2–3.5 kg.

Anatomical methods

Anatomical dissection of 7 formalin-embalmed specimens was employed to determine the parameters of the mechanical model of the masticatory system, such as the lines of action and physiological cross sections of the muscles and the coordinates of bite points and jaw joints, as previously described (Weijs *et al.* 1987). The area between the ramus of the mandible and the mastoid region of the skull, together with the infratemporal fossa, was also studied by dissection.

The histological structure of these regions was studied in a series of sections. A young (3½ week) rabbit was killed by an overdose of sodium pentobarbitone and perfused with 4% formaldehyde; the head was subsequently decalcified in EDTA (ethylenediamine tetra-acetic acid) and embedded in celloidin. Horizontal serial sections, 60 µm thick, of the entire head were made and stained alternatively with haematoxylin/azoploxine and Van Gieson (modified after de Blok, 1982).

Recording of masticatory movements

Mastication of commercial pellets, pieces of hay and small cubes of carrot was studied in four young and three adult animals by cineradiography. An X-ray tube operated at a voltage of approximately 70 KV was used in combination with an image intensifier; the tube-film distance was 1 m and the object-screen distance about 10 cm. The screen of the image intensifier was filmed (16 mm cinefilm) at 50 frames/second. Both lateral and horizontal views were examined. Skulls and mandibles of the experimental animals had been provided with metallic markers. The animals were anaesthetised with sodium pentobarbitone at least 48 hours before the recording sessions for the insertion of markers, four in the skull and four in the mandible. We used steel balls (1 mm diameter) glued to the calvaria, amalgam fillings, placed in upper and lower incisors, in the symphyseal region of the mandible and the zygomatic arch and sometimes very small screws (dental retention pins). The frames were projected by a stop-frame projector on an *x-y* tablet (resolution 0.15 mm; final magnification 2–4 times) and the position of all markers was recorded.

For each animal and food type, lateral films of two regular masticatory sequences, each comprising 400 frames (15–20 masticatory cycles) were analysed frame by frame. Jaw opening is a movement in the median plane. During closing there is an initial

movement of the jaw to the working side, followed by a reverse movement. As this movement is relatively small, amounting to only 3–5° (Weijs & Dantuma, 1981) its distortional effect upon the pathway of the sagittally projected markers is negligible. This is obvious because opening and closing paths are usually identical and always parallel. From the selected sequences the CR for the opening and closing movement was located as follows. Three markers on the skull were used to define a skull coordinate system. This is defined by the occlusal plane of the cheek teeth and the contact surfaces on the skull of the two jaw joints. The point halfway between the contact surfaces is the origin, the line connecting them the y -axis. The anteroposterior x -axis is parallel to the occlusal plane, the z -axis is vertical. A plot was then made of the position of the mandibular markers in all frames. The mid-perpendiculars of the resulting superimposed trajectories were constructed by eye and the position of the CR was estimated from the points of intersection of these lines (Fig. 3).

Computer model of jaw mechanics

To investigate the possible effects of a changed CR upon the jaw muscles we used a previously described (Weijs *et al.* 1987) three dimensional model of the masticatory system. Briefly, the jaw muscles are represented geometrically by a set of 30 force vectors. The direction of each vector is determined by the origin and insertion of the muscle portion it represents. A movement of the mandible about a certain CR changes the direction of the vector and the length of the muscle. Both the passive elastic force and the active, maximal isometric force were estimated. They depend on the sarcomere length of the muscle concerned which is known for the closed jaw position (Weijs & van der Wielen-Drent, 1982, 1983). For all other jaw positions they could be calculated from the changed distance between the origin and insertion. The relationship between sarcomere length and maximal isometric tetanic tension was modelled according to the data of Muhl *et al.* (1978). The passive force (F_p) of a muscle at a specific sarcomere length was estimated according to Woittiez *et al.* (1986) as

$$F_p = a \cdot F_{tw} \cdot \exp \left[c \frac{SL - SL_0}{SL_0} \times 100 \right],$$

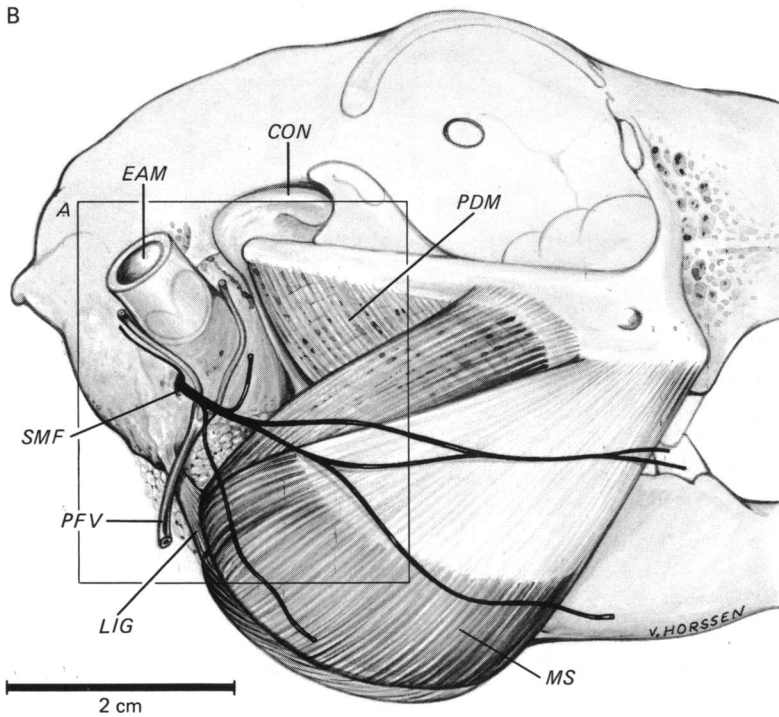
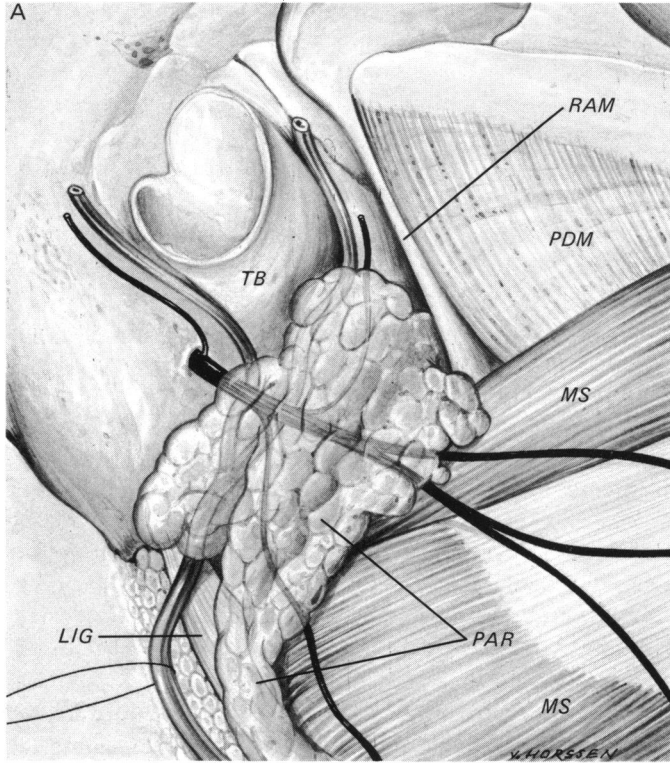
where a is a constant, F_{tw} the maximum isometric twitch tension, c a constant (called $bF\%$ by the above-mentioned authors), SL sarcomere length and SL_0 the optimum sarcomere length (2.78 μm , Muhl *et al.* 1978). The maximum tetanic force (F_{tet}) was estimated as 30 N per cm^2 of cross sectional area of muscle and F_{tw} was taken as 0.1 F_{tet} (Muhl *et al.* 1978).

The model predicts the magnitude of all the muscle forces and moments about the y -axis of the skull coordinate system as a function of gape angle. Model output is the total moment about this axis due to passive elasticity together with the total moment due to maximal isometric contraction of the jaw-closing muscles.

The constants a and c were assumed to be equal for all muscles and were estimated as described below.

Measurement of passive resistance

To determine the resistance to opening offered by the passive elastic forces of the jaw muscles two young and two adult rabbits were anaesthetised with sodium pentobarbitone and each provided with four metallic markers, two on the skull and two on the jaw. The animals were then killed by an overdose of sodium pentobarbitone and decapitated. The head was firmly mounted in a stereotactic apparatus with its



mid-sagittal plane in a horizontal position. A flexible wire connected the lower incisors to a force transducer mounted on a translation stage, movable along the direction of the force. The force was exerted in a caudoventral direction; the angle between the maxillary occlusal plane and the force was approximately 60°. The distance between the incisors and the transducer was about 1 m, so that displacement of the transducer did not cause a notable change of angle. The force signal was amplified by a bridge amplifier and output read from an analogue meter. The accuracy of the force measurement was better than 1 g, the linearity of the transducer better than 1%. The mandible was opened and allowed to close stepwise by moving the translation stage. After one minute of stabilisation time the force was read and a lateral radiograph was taken.

The angle of gape is defined as the angle between the upper and lower occlusal surfaces of the cheek teeth. It was measured from the radiographs. Changes in gape could be measured with an accuracy better than 1% by using the angle between the line connecting the skull markers and the line connecting the mandibular markers. The position of the CR was determined separately for the opening and closing movement. It is the point of intersection of the mid-perpendiculars to the trajectories of the two mandibular markers.

In each animal a series of 20–30 measurements, consisting of several opening and closing movements, was obtained within 90 minutes after death. The resistance against jaw opening was expressed by the moment (force times lever arm) about the fixed y -axis of the skull coordinate system. The lever arm is the shortest distance between the line of action of the external force and the jaw joint, measured in lateral projection. Model-generated gape-passive moment curves for various values of the parameters a and c of the elastic force equation were compared to the experimentally obtained curves. The values producing the best fit to the experimental data of individual animals were adopted. The mean values for infant and adult animals were used for further model simulations.

Finally, the jaw muscles were cut and the experiments and all measurements repeated to determine the combined effect of the passive behaviour of the temporomandibular joint and other soft tissues around the mandible.

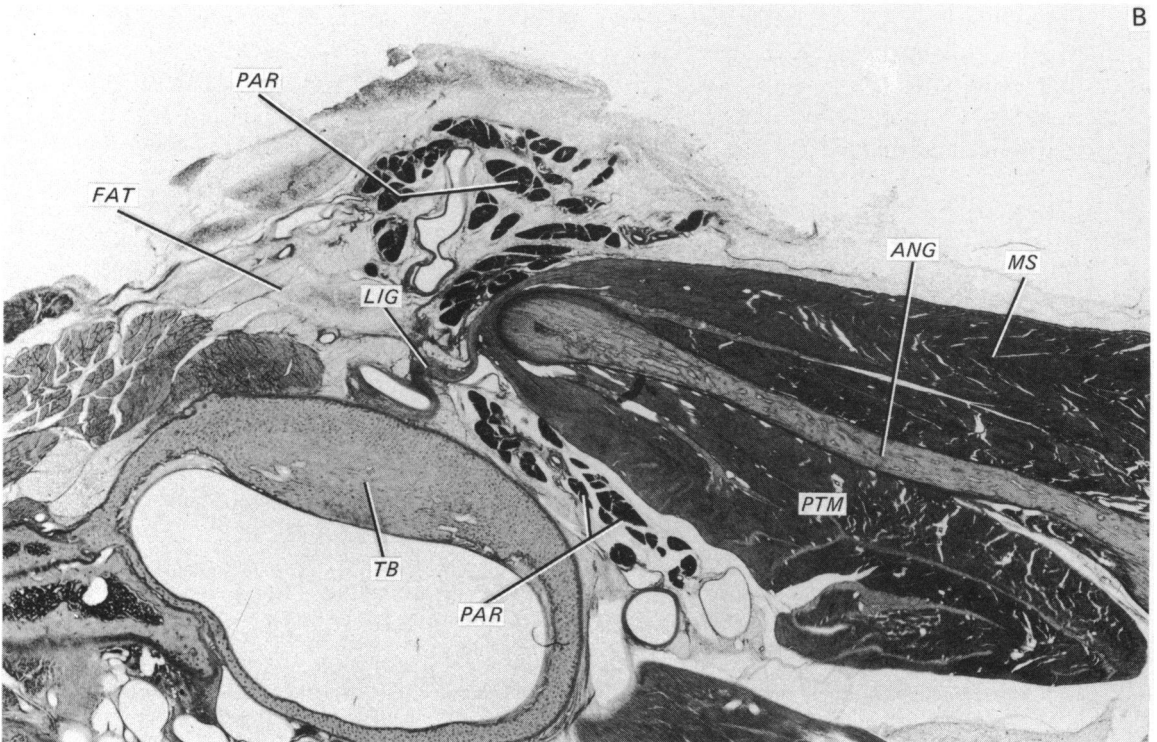
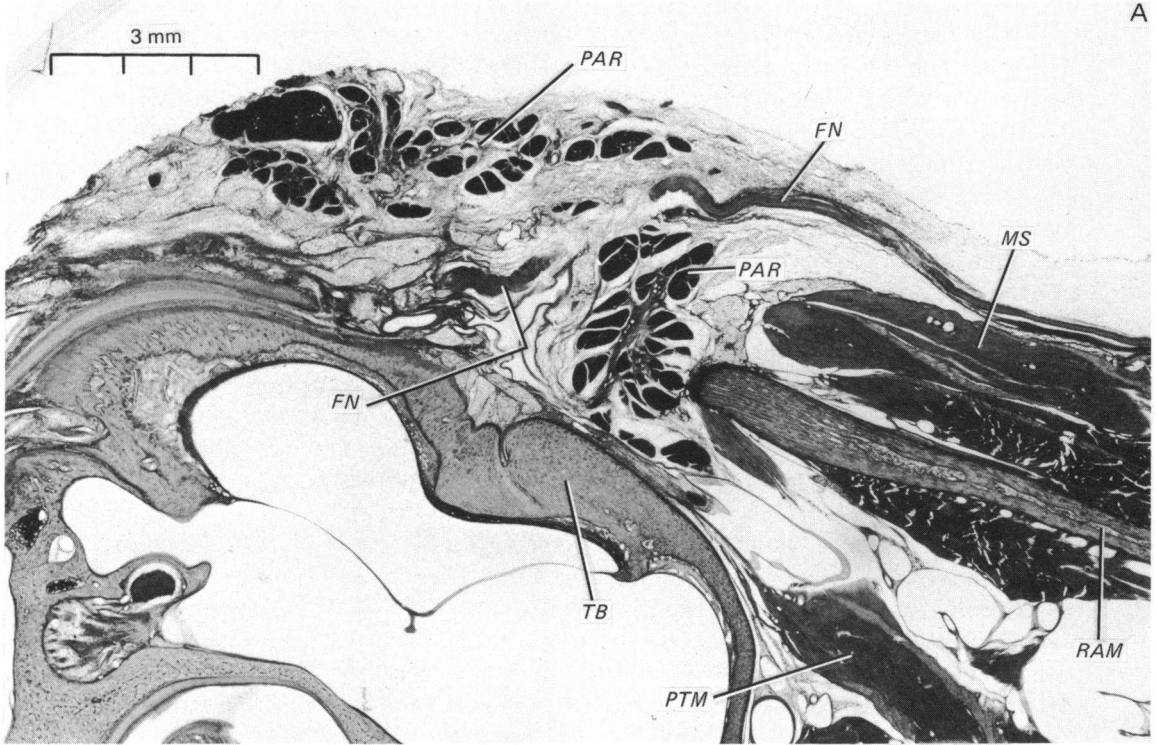
RESULTS

Anatomy of the retromandibular region

The retromandibular region is here defined as the area between the ascending ramus of the mandible and the lateral wall of the tympanic bulla. Lateral views of the region (Fig. 1) and two horizontal microscopic sections (Fig. 2) are shown; the first section is at the level of the posterior tip of the jaw angle, the second about 3 mm more superior, at the level of the stylomastoid foramen.

Anteriorly, the region is bounded by the ascending ramus of the mandible sandwiched between the insertions of four jaw muscles. Superiorly, the lateral aspect

Fig. 1(A–B). Superficial and deep dissections of the parotideomasseteric region in an adult rabbit. (A) Superficial dissection, showing the parotid gland (*PAR*) in its relationship to the mandibular ramus (*RAM*), tympanic bulla (*TB*), superficial masseter (*MS*) and posterior deep masseter (*PDM*). The gland has been represented as being semi-transparent to illustrate the topography of the underlying structures. Superiorly, the superficial portion of the parotid gland is broadly connected to a deep portion behind the mandible; inferiorly, there is no such connection. (B) General view of the same region after removal of most of the parotid gland, showing the course of the facial nerve after its exit from the stylomastoid foramen (*SMF*), the posterior facial vein (*PFV*) and the ligament described in the text (*LIG*). Behind the ligament lies loose adipose tissue. *CON*, mandibular condyle; *EAM*, external auditory meatus.



of the jaw is covered by the posterior deep masseter, the medial aspect by the inferior head of the lateral pterygoid. Inferiorly, the superficial masseter attaches to the lateral side and the medial pterygoid to the medial side of the angular process. For a complete description of these muscles see Weijs & Dantuma (1981).

Posteriorly the tympanic bulla and bony and cartilaginous portions of the external auditory meatus border the retromandibular region. The tympanic bulla is braced posteriorly by a mastoid process and by a paroccipital (or parajugular) process of the exoccipital bone. An obvious styloid process is lacking (Frick & Heckmann, 1955). Below the bulla, the sternocleidomastoid muscle, originating from the mastoid process, borders the region. The region has a somewhat rhomboid shape in lateral view; in horizontal section, it appears as a narrow slit.

The parotid gland is found directly below the skin, platysma and subcutaneous fat, lateral to the masseter and sternocleidomastoid muscles and in the gap between these muscles. The rest of the gland lies in the narrow slit between the medial pterygoid muscle and tympanic bulla. At the level of the superior half of the ascending ramus the superficial and deep portions of the gland are broadly connected so that the glandular tissue completely surrounds the posterior border of the ramus. More inferiorly, at the level of the stylomastoid foramen (Fig. 2A) the facial nerve and adjoining connective tissue completely separate the two portions. Still lower (Fig. 2B) only a little glandular tissue is present in the slit and this tissue is not continuous with the superficial portion.

The superficial region of the parotid gland is traversed by the posterior facial vein (Craigie, 1960) receiving tributaries from the ear, superficial masseteric region and superficial temporal region. The gland is further crossed by the facial nerve. This nerve emerges from the stylomastoid foramen, situated between the mastoid process and tympanic bulla on the lateral aspect of this bone. It gives off a number of branches (Fig. 1; see Meinertz, 1936, for details). The buccal branch of the facial nerve traverses the retromandibular region below the superficial portion of the parotid gland. It runs a straight course, almost parallel to the median plane. It emerges from below the parotid gland at the surface of the masseter muscle.

Deep to the superficial portion of the parotid gland lies a broad ligament about 5 mm long in adult animals, connecting the posterior tip of the angular process to the lateral surface of the tympanic bulla, just below the stylomastoid foramen (Figs 1, 2). If the jaw is completely closed, the ligament is almost taut. It then runs anteriorly, ventrally (downward) and laterally from the skull to the mandible. This tympano-mandibular ligament is entirely surrounded by loose adipose tissue.

The inferior alveolar nerve runs obliquely forward and downward from the dorsally situated foramen ovale to the mandibular foramen. The latter is situated approximately at the same vertical level as the natural centre of rotation (see next section), but about 1 cm (infants) to 1.7 cm (adults) further forward.

Natural jaw opening and closing

A typical example of the paths taken by four mandibular markers relative to the skull is shown (Fig. 3). It represents 16 chewing cycles for carrot (adult animal) with

Fig. 2(A-B). Microscopic sections of the retromandibular region. (A) At a level just above the stylomastoid foramen, 3 mm superior to the tip of the angular process (*ANG* in *B*). The facial nerve (*FN*) can be seen traversing the parotid gland (*PAR*) and separating it into a superficial and a deep portion. (B) At the level of the posterior tip of the angular process and the ligament (*LIG*) between tympanic bulla and angular process. Behind the mandible loose adipose tissue is seen (*FAT*). *PTM*, medial pterygoid muscle; for other abbreviations, see Fig. 1.

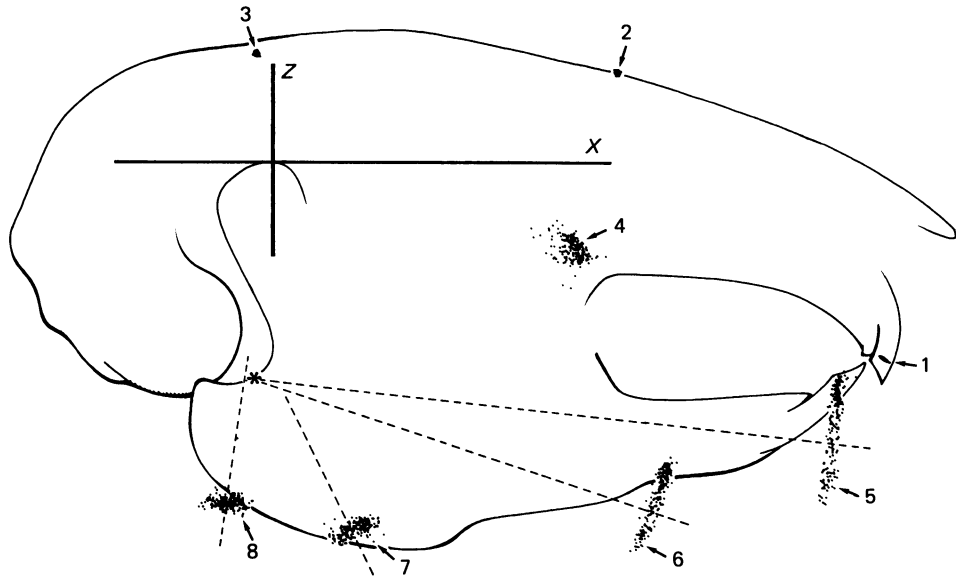


Fig. 3. Positions of four skull markers (1-4) and four mandibular markers (5-8) in 198 movie frames of a masticatory sequence consisting of 18 chewing cycles of carrot in an adult rabbit. From the trajectories of the mandibular markers, mid-perpendiculars are constructed. The intersections of these lines determine the centre of rotation of the jaw (asterisk). Markers 1, 2 and 3 were used for superposition of the skulls. Marker positions; 1, upper incisor; 2 and 3, cranial vault; 4, zygomatic arch; 5, lower incisor; 6, symphysis; 7 and 8, left and right lower margin of mandible. The coordinate system, described in the text is shown.

Table 1. *Position of centre of rotation for jaw opening/closing, expressed as horizontal (x) and vertical (z) distance from temporomandibular joint ($\bar{x} \pm S.E.M.$ in cm)*

| Food | Infant | | | Adult | | |
|--------|--------|------------------|------------------|-------|------------------|------------------|
| | n | x | z | n | x | z |
| Pellet | 5 | -0.24 ± 0.11 | -1.34 ± 0.13 | 3 | -0.13 ± 0.03 | -2.35 ± 0.12 |
| Hay | 4 | -0.30 ± 0.09 | -1.09 ± 0.16 | 3 | -0.44 ± 0.27 | -2.09 ± 0.03 |
| Carrot | 4 | -0.10 ± 0.07 | -1.34 ± 0.16 | 3 | -0.31 ± 0.25 | -2.24 ± 0.17 |

an average maximal gape of 10.8° . The skulls are superimposed using markers 1, 2 and 3. Marker 4 is at the zygomatic arch and is very sensitive to skull rotation. For this reason the marker position shows scatter. Markers 5, 6, 7 and 8 are located at the left lower incisor, symphyseal region and right and left mandibular angles, respectively. The Figure shows how the CR is determined. No signs were observed of change in direction of the trajectories of the markers in any of these plots. As the measurement noise, apparent from the scatter about the trajectories, is small one may conclude that the jaw opens and closes about the same relatively stable CR.

Table 1 gives the average positions of the CR determined in four infant and three adult animals, masticating pieces of carrot, hay and pellets. The positions are defined relative to the skull coordinate system. There appears to be no significant difference (*t*-test) in CR position with different foods. Between the age groups there is a difference, but the relative position of the CR is the same. It is slightly behind and well

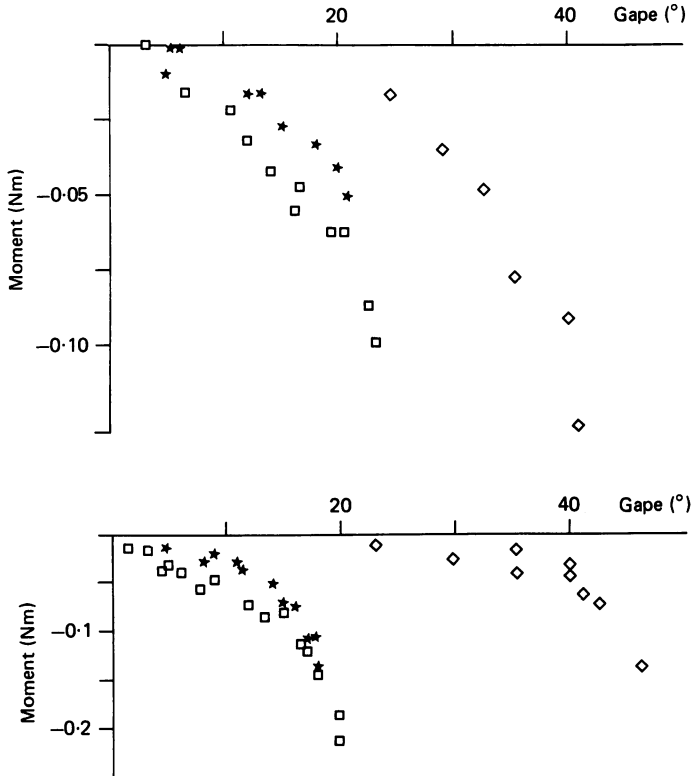


Fig. 4. Passive jaw-closing moment (in Nm) as a function of the gape (in degrees) in an infant (top) and an adult (bottom) animal. Symbols \square refer to values, obtained during jaw opening, \star to values, found during closing. Values obtained during opening and closing after the jaw muscles had been cut are shown as \diamond .

below (1.3 cm in infants and 2.2 cm in adults) the temporomandibular joint. In both age groups, the average CR is located at the posterior margin of the ascending ramus, near the posterior tip of the angular process. This position is very constant between animals, between foods and between chewing cycles. The variances (Table 1) are reflections of measurement error and size differences.

Passive jaw-closing moment

Examples of results of passive jaw-opening experiments are shown for an infant and an adult animal (Fig. 4). After an increase of gape, the closing moment is high initially and then drops to a lower equilibrium value in about one minute. After a decrease, the moment tends to creep to an equilibrium value which is somewhat higher than the initial value. The graphs show considerable hysteresis. Under the experimental conditions jaw opening occurs about a CR located 1.3 cm (infants) and 2.3 cm (adults) below the condyle; normally there is no change in position of this centre during jaw opening.

The mean estimates for the constants a and c , describing the passive behaviour of the individual muscle portions are as follows: $a = 0.056$ in young and $a = 0.014$ in adults; $c = 0.06$ in both groups. Hence the linear factor a is smaller in adults, pointing

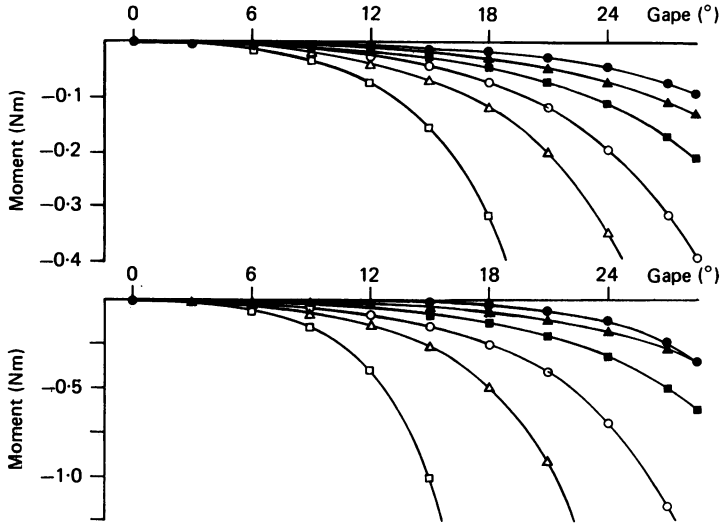


Fig. 5. Passive jaw-closing moment at different gapes, obtained by rotation about different CRs in infant (top) and adult (bottom) animals. The CR position varies between the level of the temporomandibular joint (\square) and the lower border of the mandible (\bullet). The vertical distance between CR and the joint is 0.00 (\square), 0.64 (\triangle), 0.96 (\circ), 1.28 (\blacksquare), 1.60 (\blacktriangle) and 1.92 (\bullet) cm for infants and 0.00, 1.12, 1.68, 2.23, 2.79 and 3.35 cm (same sequence of symbols) for adults. In both age groups the graph marked by \blacksquare represents the results in case of rotation about the natural CR. For clearness only half the data points are shown as symbols.

to a decreased stiffness. It could be assumed that the skin does not contribute to the closing moment as it is loose in the area of lips and cheeks in the observed gape range.

After sectioning of the jaw muscles the jaw can be opened to a gape of more than 40° in young and $30\text{--}40^\circ$ in adult animals with little resistance (Fig. 4). Hence the temporomandibular joint does not play a role in determining the passive resistance to jaw opening in the intact animal.

Model predictions

The mathematical model has been used to calculate (1) the sum of the passive elastic moments generated by the muscles at increasing gapes and (2) the active isometric forces that can be maximally exerted by the combined jaw-closing muscles. To evaluate the role of the centre of rotation (CR), rotations about six different vertical CR positions between the contact area of the temporomandibular joint and the lower margin of the mandible were simulated.

Passive jaw-closing moment

The predictions for the passive jaw-closing moment at different gapes make clear that opening about a CR located at the condyle leads to large passive closing moments beyond 10° of gape (Fig. 5). For lower CR positions the passive moment decreases progressively but a position below the observed CR contributes only slightly to the further reduction of passive resistance. Comparison of the age groups shows that in adults the system resists jaw opening more strongly than in infants at comparable gapes and CR positions. Comparison of contributions of the individual muscles (not shown) leads to the conclusion that the well-developed superficial masseter and medial pterygoid muscles contribute most to the closing moment.

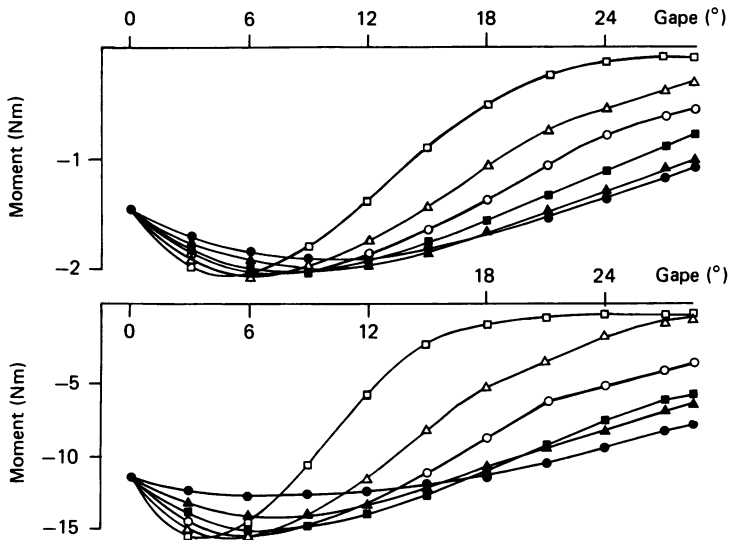


Fig. 6. Maximum active jaw-closing moment at different gapes and positions of the CR for infant (top) and adult (bottom) animals. Symbols for CR positions as in Fig. 5.

Active jaw-closing moment

The position of the CR has a considerable effect upon the combined jaw-closing moment, generated by maximal isometric contraction of the masseter, temporal and medial pterygoid muscles (Fig. 6). With the jaw closed the muscles are below optimum length. The increase and subsequent decrease in force at increasing gapes is due to the progressive stretching of the contractile components of the muscles. The curves for different CRs have a common starting point at zero gape (no rotation). In most muscles sarcomere length reaches an optimum between 3–9° gape. If the mandible rotates about a CR at or near the condyle, most muscles are stretched quickly so that the largest jaw-closing moment is reached at a relatively small gape. At larger gapes reached by further rotation about such CRs the moment declines sharply. The animals would then be unable to bite hard in large objects. The location of the real CR is such that muscle stretching is minimised. This results in an optimum closing moment at a relatively large gape and a flat gape–moment curve. Further downward displacement of the CR hardly leads to further reduction of muscle stretching. The effects of CR displacement upon active tension are more marked in adults than in infants because of the relatively short fibres in the adults.

DISCUSSION

Model estimates and experimental results

The cineradiographic data of normal mastication unequivocally demonstrate the presence of a stable centre of rotation (CR) for masticatory opening/closing movements in a gape range between 0 and 15°. The position of the CR, more than halfway between the temporomandibular joint and the lower margin of the mandible is independent of animal size and food. An artificial external opening force tends to rotate the jaw about the same CR in a freshly killed animal.

The maximum gape is limited by the elastic forces of the jaw-closing muscles. With intact muscles the jaw can be opened 20–25°; the skin of the cheeks and lips remains

loose under those conditions. After all muscle bellies have been cut, the system offers little resistance against opening at gapes between 0–20° and the jaw can be opened to gapes of 30–40°. In adult jaw muscles the muscle fibres occupy a smaller percentage of total muscle length than they do in infants (Weijs *et al.* 1987). The model used therefore predicted that the increase in passive resistance against opening would be steeper in adults than in infants. The experimental curves were steeper but the difference was smaller than expected. This leads us to assume that infant muscles are stiffer than those of the adult, an observation confirmed by data from the literature for rat leg muscles (Woittiez *et al.* 1986; de Koning, van der Molen, Woittiez & Huijing, 1987). We found similar values for the constants describing the length–passive tension relationship as did these authors.

By adjusting elastic parameters the predicted passive jaw-closing moment was fitted to the experimental data. The model predictions for rotation about simulated CRs are based on the assumption that the same elastic constants apply to all muscles in an animal of a certain age. As the constants depend not only on the properties of the muscle fibres but also on the length of the tendon, there may be some variation among muscles with respect to these values, thus biasing the results obtained.

It has been shown before (Weijs & Van der Wielen-Drent, 1982, 1983) that accurate predictions of sarcomere length can be made, based on geometric assumptions. However, the model neglects the effects of angular attachments of muscle fibres to tendons. Muhl (1982) showed experimentally that the fibres of the rabbit digastric lengthen 23% less than the displacement of its tendon. As the pinnation angles of the jaw-closing muscles are relatively small, and not greatly different among the different muscles, the model results will not be greatly influenced by this effect. It acts in the same direction for all jaw-closers and leads to some overestimation of passive tensions occurring at a specific gape. Active tension was estimated from sarcomere length by using the data of Muhl *et al.* (1978) for the rabbit digastric muscle. This ignores possible differences in intrinsic strength between muscles. However, Powell *et al.* (1984) showed that intrinsic strength was the same in a number of guinea-pig leg muscles with different fibre compositions.

The functional relevance of CR position

Between the stylomastoid foramen and the surface of the masseter muscle the facial nerve crosses the retromandibular space at the level of the CR. Hence, this segment of the nerve is not subjected to length changes. It is, however, difficult to believe that the position of the nerve could not be adjusted to another location of the CR. This also applies to the inferior alveolar nerve. As long as the CR is located above the lower margin of the jaw, the line connecting the CR and the mandibular foramen is at a small angle to the nerve and the nerve is not greatly stretched during opening. The distribution of parotid gland tissue behind the ramus seems to be dictated by the amount of displacement of the posterior border of the ramus. Below the observed CR, opening causes a backward displacement of this border and glandular tissue is replaced by loose adipose tissue. The distribution of the glandular tissue again seems to be secondarily determined by the position of the CR.

Displacement of the CR towards the temporomandibular joint greatly increases the stretch of the fibres of the jaw-closers during opening. Consequently, the closing muscles offer an increasing passive resistance against opening. The effect becomes measurable at gapes above 5°; at gapes above 6–8° the elastic closing moment reaches values of more than 10% of the maximum possible moment generated by the jaw-

openers (data not shown). As maximal gapes attained at natural mastication amount to 10–15° (Weijs & Dantuma, 1981) it is obvious that only rotation about the observed CR avoids the necessity for jaw-openers to counteract the passive resistance of the closers.

A second effect of upward displacement of the CR, with resulting muscle fibre stretch, would be a reduction of the maximum isometric tension of the jaw-closers and a restriction of the bite force of the animal at large gapes. This effect is less dramatic than the former and occurs only at gapes larger than 12°. Carlson (1977), in a craniometric analysis of jaw opening in the Macaque monkey, found that the location of the CR below the condyle reduced the extension of the superficial masseter muscle and made possible larger bite forces at larger gapes. He assumed that optimum length of the sarcomeres was attained with a closed jaw. This is not true for many animals (Nordstrom & Yemm, 1974; Mackenna & Türker, 1978; Manns, Miralles & Palazzi, 1979) and may have led to overestimation of the length–tension effects. Furthermore he supposed that a change in length of the muscle is evenly distributed over the entire muscle instead of over the length of its fibres only. This must have led to an underestimation of the effect. Nevertheless his conclusions are supported by our study. However, we attribute a larger significance to the avoidance of passive elastic forces than to the maintenance of active forces, as the first effect is much larger in the natural range of jaw movements.

Displacement of the CR from its actual position towards the lower border of the jaw has a negligible effect upon the passive and active forces of the muscles. It would imply an increase of the already large protrusion of the condyle during opening. It can be concluded that CR position is as low as necessary to minimise the passive forces in the jaw-closing muscles, and simultaneously allows maximal active forces to be generated over a large range of gapes.

In their comparative analysis of jaw opening, Herring & Herring (1974) argue that masseter stretch is maximal if the ratio of distances between origin and jaw joint on the one hand and insertion and jaw joint on the other is equal to unity. This would be true if the joint coincides with the CR. For animals needing large chewing pressures such a morphology is advantageous because it maximises the lever arm of the masseter and medial pterygoid muscles and hence the bite force. This is particularly so in lagomorphs and ungulates (Radinsky, 1985; Turnbull, 1970) which concentrate their masticatory strength in these muscles; it may also apply to primates, including man. Contrary to the suggestion of Grant (1973) the leverage of the muscles and the magnitude of the bite force are solely determined by the point of application of the reaction forces at the teeth and at the jaw joint. Jaw movements on the other hand, depend on the position of the CR, not of the jaw joint. The significance of a CR position away from the joint resides in the decoupling of opposing functional demands for maximal leverage and maximal jaw opening. To meet the first, the jaw joint is in a location some distance from the muscles; the second demand is satisfied by lowering the CR to reach a position close to the insertion areas of the muscles. In pure hinge joints, such as carnivore jaws joints, such a mechanism is impossible.

A second mechanism to reduce passive stress in the closing muscles is an adjustment of sarcomere length in such a way that the fibres are below optimum length with a closed jaw. In contrast to Herring, Grimm & Grimm (1984) we have suggested that sarcomere length is not adjusted to reach optimum values during maximum activity but to avoid overextension at maximal jaw opening (Weijs & Van der Wielen-Drent, 1983).

Mechanical determinants for the CR

The preferred rotation of the mandible about a fixed CR in both conscious animals and postmortem experiments suggests control by passive elastic forces. However, some condylar protrusion is possible without jaw opening. Baragar & Osborn (1984) showed by using a mathematical model for the human mandible that the range of movement of the condyle is determined by the shape of the cranial articulating surface of the jaw joint and the presence of two or three ligaments. At increasing amounts of jaw opening the freedom of movements becomes more restricted. A similar situation may occur in the rabbit system. At small gapes additional control mechanisms are needed to keep the CR in a constant position. Such control forces could be provided by the lateral pterygoid, active during opening, and the posterior deep masseter, active during closing (Weijs & Dantuma, 1981; Weijs & Muhl, 1987).

As long as the structures of the temporomandibular joint do not offer any restriction, the mandible will move in response to an opening or a closing force in such a way that the evoked elastic forces and the total elastic energy stored in the jaw muscles is minimised; this results in rotation about the observed CR. After all the jaw muscles have been sectioned, an opening path is obtained which lies posterior to the path in the intact animals. This corroborates the view that passive muscular forces determine CR position. The jaw can then be opened further and this suggests that the muscles also limit the amplitude of the movement. The tympanomandibular ligament described above is almost tight in the closed jaw position and then limits condylar protrusion like the stylomandibular ligament in man (Burch, 1970). A combination of opening and protrusion can possibly keep the ligament tight. It would then set a limit to the amount of protrusion, possible at each gape and thus to the lowest position of the CR. The ligament would also limit the maximum possible lateral deviation of the mandible. The question of possible guidance of opening and closing movements by this ligament can, however, not be answered without further experimental research.

This work indicates that the elastic forces of the jaw-closers play a major role both in guiding and restricting mandibular motion. The temporomandibular joint capsule lacks clearcut reinforcements and does not seem to be important in this respect. Interestingly, the role of the joint capsule and associated ligaments in the human masticatory system has been strongly emphasised, while the role of the muscles, as far as we are aware, has never been considered.

SUMMARY

In the rabbit, jaw opening and closing occurs in combination with condylar protrusion and retraction. Consequently the centre of rotation (CR) for the movement lies in the inferior portion of the ascending ramus of the mandible, far below the condyle. This location is stable and independent of the type of food being chewed and the age of the animal. The topography of the soft tissues at the posterior border of the ramus is adapted to the movement pattern. The facial nerve crosses the space between skull and mandible at the level of the CR. The parotid gland lies behind the ramus between condyle and CR; below the CR, the gland is replaced by loose adipose tissue. A computer model was used to demonstrate that the location of the CR determines the amount of stretch of the large masseter and medial pterygoid muscles. Using parameters for passive elastic behaviour of muscle, obtained by postmortem measurements, it can be shown that the normal CR position minimises muscle stretch and passive elastic forces. Even a small upward displacement of the CR causes a

significant amount of resistance in the jaw-closers at gapes comparable to those reached in natural mastication. A second, less dramatic effect of increased muscle stretch is a sharper decline of maximum possible active closing force, due to the interrelationship of fibre length and isometric tension. In young animals, the muscle fibres are relatively long but stiff; in adults they are shorter, but more compliant. In both ages the CR is located in such a way that masseter and medial pterygoid stretching is minimised. The high position of the temporomandibular joint ensures a maximal leverage for the muscles mentioned above. By separating the point where the reaction forces apply (the joint) from the location of the rotational axis, maximum leverage and minimal length changes of the jaw-closing muscles are achieved simultaneously. It is further suggested that elastic muscular forces play a role in determining the position of the CR.

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