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MANDIBULAR TRANSLATION IN
VERTEBRATE JAW MECHANICS**

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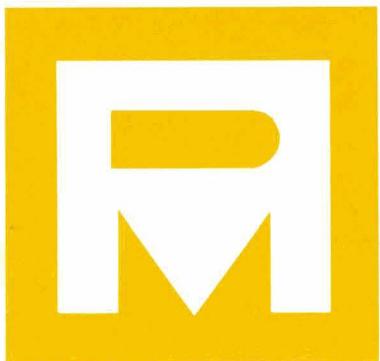
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ABSTRACT

Fore-aft translatory freedom of jaw articulation and alignment of muscle fibers with the bite point make the chief adductor muscles of most reptile and mammal jaws mechanically very efficient. The force generated by the adductor muscles acts directly against the food at the bite point with no reaction force wasted at the jaw joint. The jaw is functionally a link and not a lever.

Translatory freedom of the jaw joint is provided either by a sliding jaw joint (in most mammals, birds and some reptiles) or by a two-jointed jaw suspension (in most lizards and snakes).

ABBREVIATIONS

a	moment arm of F_t
A	human jaw articulation
A_h	quadrate-jaw articulation of lizard
A_s	quadrate-cranium articulation of lizard
b	moment arm of F_b
B	bite point considered in the analysis
F_a	force of contraction of the mandibular adductor muscles of lizards
F_a'	equal and opposite reaction force to F_a, equal to the bite force at B
F_b	bite force at B
f_m	component of F_m perpendicular to bite force F_b
F_m	force of contraction of human masseter muscle
F_r	reaction force at the jaw joint
f_t	component of F_t perpendicular to bite force F_b
F_t	force of contraction of human temporalis muscle
F_t'	equal and opposite reaction force to F_t, equal to the bite force at B
q	lizard quadrate bone

INTRODUCTION

Many recent papers interpret the mechanics of vertebrate jaws by treating the jaw as a functional lever rotating about the jaw articulation (see Turnbull, 1970; Barghusen and Hopson, 1970; Kemp, 1969; Crompton and Hiiemäe, 1969; Szalay, 1969; Crompton and Hotton, 1967; Ostrom, 1964; Davis, 1964; Crompton, 1963a,b; Olson, 1961; Schaeffer and Rosen, 1961; Smith and Savage, 1959). This interpretation is illustrated in Fig. 1A. The relatively long length of the bite lever arm and the great amount of force wasted as reaction force at the jaw joint make this proposed mechanical system generally very inefficient.
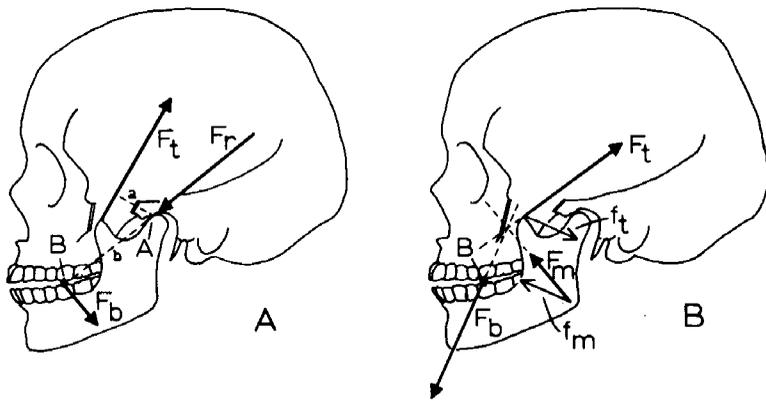

FIG. 1. Human skull illustrating previous interpretations of jaw mechanics: A. Lever interpretation. F_t produces a clockwise turning moment a $\times$ F_t opposing the counterclockwise turning moment b $\times$ F_b produced at the bite point B. In equilibrium the force F_r acts on the jaw at the articulation A. For clarity vector F_r is shown with its head at the point of application. The bite force at B is approximately ⅓ the muscle force applied to the jaw. B. Previous nonlever interpretation (after Robinson, 1946). The lines of action of F_t, F_m, and F_b all pass through a common point. Components of force f_t and f_m act against each other. The bite force at B is approximately ⅔ the muscle force applied to the jaw by $F_t + F_m$. This interpretation also requires that F_t be oriented unreasonably far back on the cranium.

Alternatively, the a priori assumption that there is no reaction force at the jaw joint in some mammals and mammal-like reptiles has led to the interpretation of relative muscle forces illustrated in Figure 1B. (This interpretation has been proposed by Robinson,

1946; Smith and Savage, 1959; and Crompton, 1963a, b.) This system is inefficient because major components of the temporalis and masseter muscle forces act against each other.

The commonly accepted hypothesis that the mammalian jaw is functionally a lever implies that the jaw joint, the fulcrum of the lever system, is fixed with respect to the cranium. In most reptiles, birds, and mammals this is not true. The lower jaw is generally free to translate fore-aft with respect to the cranium by either of two mechanisms. Translatory freedom is provided either by a sliding jaw joint (present in most mammals, birds, turtles, and *Sphenodon*) or by a two-jointed jaw suspension (streptostylic quadrate present in most lizards and snakes). The sliding jaw joint mechanism is illustrated in this paper by a human skull; the two-jointed jaw suspension is illustrated by the lizard *Ctenosaura*.

THE SLIDING JAW JOINT

The jaw joint in man (Fig. 2) consists of the articular fossa of the temporal bone above, an intermediate fibrocartilagenous articular disk, and the mandibular condyle below. The mandibular condyle and articular disk are separated by a synovial cavity permitting the
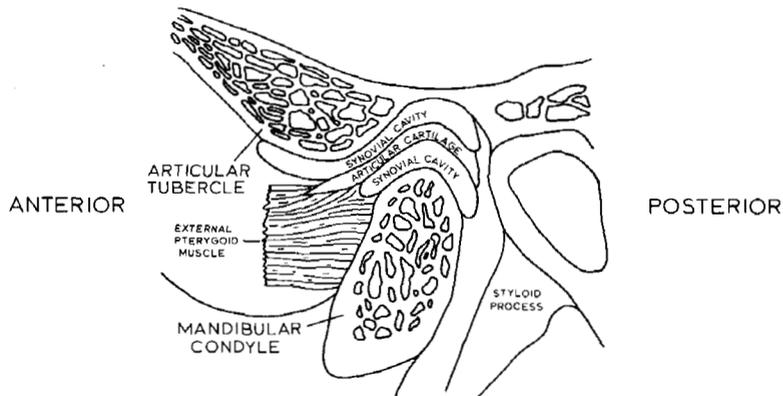

FIG. 2. Parasagittal section through the human jaw articulation. As the jaw is protruded by contraction of the external pterygoid muscle, the mandibular condyle slides forward on the articular tubercle. See text for further discussion.

condyle to rotate with respect to the articular disk. Both mandibular condyle and articular disk form the insertion for the external pterygoid muscle. The articular disk and temporal bone are also separated by a synovial cavity, permitting the articular disk-mandibular condyle assembly to translate forward when the external pterygoid muscle contracts. Mandibular depression-elevation is accompanied by simultaneous fore-aft translation of the mandible (Rees, 1954).

The chief muscle adducting the human jaw is the temporalis; it originates from the side of the cranium and inserts on the coronoid process of the mandible. The areas of origin and insertion of the temporalis muscle are shown in Figure 3B. As is shown in Figure
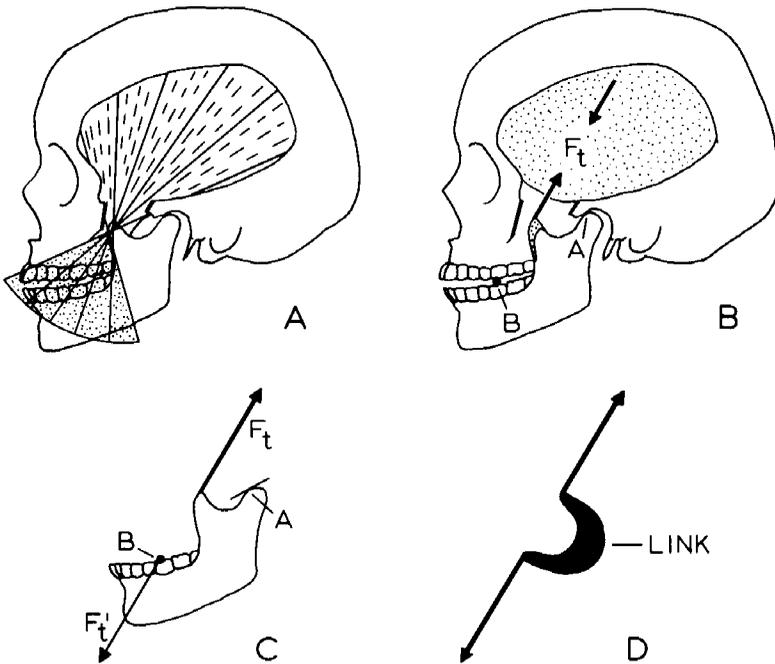
FIG. 3. Mechanics of human temporalis muscle. A. Orientation of temporalis muscle fibers. Collectively the envelope of temporalis fibers is aligned with the entire tooth row. B. Origin and insertion of temporalis muscle shown stippled. F_t represents the maximum force of contraction of the entire temporalis muscle. F_t is aligned with a bite point between the upper and lower first molars. C. Diagram of forces acting on the mandible. The bite force F_t' is equal to the muscle force F_t. D. Diagrammatic representation of the mandible as a link between forces; see Figure 3C.

3A, the muscle fibers of the temporalis muscle are arrayed fan-like on the side of the skull. The envelope of temporalis fibers projected through the insertion on the coronoid includes the entire tooth row; thus some muscle fibers are aligned with any potential bite point along the tooth row. The maximum force F_t produced by contraction of the whole temporalis muscle will lie along a line bisecting the muscle mass. In Figure 3B, this line passes through the bite point between the upper and lower first molars.

Analyzing the mechanics on the side of chewing statically, the force F_t of contraction of the temporalis muscle acting on the mandible will be opposed by a reaction force F_t', the sum of whose components will be equal to and opposite F_t. The mandible is in contact with the cranium at two points: one through the mandibular condyle, the other through the food. Components of reaction force can only occur at these two points. In the mandibular position shown in Figure 3B, at the beginning of a bite, the mandibular condyle is separated from the cranium by a well-lubricated, low-friction plane of sliding. As the condyle is free to slide posteriorly with contraction of the temporalis muscle, an insignificant component of reaction force will occur through the mandibular condyle at the jaw joint. Virtually the entire reaction force F_t' must therefore occur at the other contact between the mandible and the cranium, i.e. through the food (Fig. 3C). The force resulting at the bite point is thus virtually equal to that produced by the muscle itself. Alignment of the temporalis origin, temporalis insertion, and the bite point, and the presence of a low-friction sliding jaw joint permit generation of a very efficient bite force by the temporalis muscle. No force is wasted as reaction force at the jaw joint. As illustrated in Figure 3D the jaw is functionally a link between two forces, rather than a lever. A simple model constructed with springs of known stretching constants and a sliding jaw articulation based on Figure 3C confirms the fact that the muscle force F_t is equal to the bite force F_t' if the jaw is free to translate until these forces are aligned.

THE TWO-JOINTED JAW SUSPENSION

The lizard jaw articulation is mechanically different, though functionally similar to the example just presented. In the lizard the jaws and cranium are separated on each side by an intermediate bone,

the quadrate (see Figure 4). The dorsal end of each quadrate is attached to bones of the cranium by an interosseus ligament permitting limited fore-aft rotation of the quadrate about the quadrate-cranium joint A_s (Oelrich, 1956). The quadrate is thus streptostylic. The quadrate articulates with the quadrate process of the pterygoid bone by a diarthrosis, permitting the quadrate to rotate fore-aft independently of the kinetic maxillary segment of the skull. Each jaw is attached to the ventral end of a quadrate by a hinge joint A_h. As the quadrates rotate about the quadrate-cranium joints the jaws translate fore-aft with respect to the cranium.

Mandibular depression in lizards is accompanied by forward rotation of the quadrates (Frazetta, 1962). As the jaws are elevated they are therefore also free to translate posteriorly. Figure 4 shows a skull of the lizard *Ctenosaura,* illustrating the orientation of the force vector F_a representing the mandibular adductor muscles and with food at a bite point B. As in the human example above, components of reaction force can only occur through the food and through the jaw joints. The quadrates are free to rotate posteriorly, furnishing little reaction force through the joint. Virtually the entire reaction force F_a' occurs through the food. The force resulting at the bite point is approximately equal to that produced by the adductor musculature itself. Alignment of the origin and insertion of the mandibular adductor muscles with the bite point, and translatory freedom of the jaw articulation permit generation of a very efficient bite force by the adductor muscles.
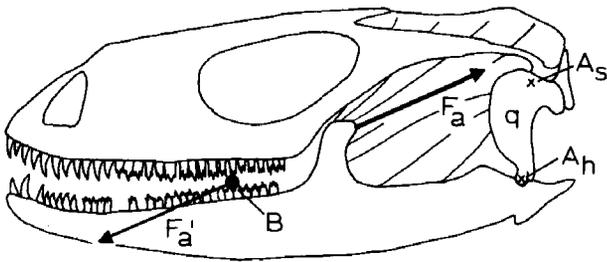

FIG. 4. Mechanics of the mandibular adductor muscles of *Ctenosaura* (skull after Oelrich, 1956). The bite force F_a' is equal to the muscle force F_a.

DISCUSSION

Two factors of jaw construction affect muscular efficiency in producing bite force. To be highly efficient, the line of action of the contracting muscles must pass directly through the food, eliminating force couples (which would have to be equilibrated either by additional muscle forces or force at the jaw joint), and the jaw joints must be free to translate, eliminating reaction force at the joints. As shown in Figures 3 and 4, and as discussed above, both these conditions are satisfied in man and in the lizard *Ctenosaura*. The coronoid process functions in both to align the fibers of the adductor muscles with the bite point. A sliding jaw joint, or rotating quadrate, minimizes the component of reaction force at the joint. During powerful biting the jaw is functionally a link, rather than a lever, between the adductor muscle force and the bite point.

The efficiency of jaw adduction described above applies particularly to orthal retraction of the jaws. Chewing in reptiles involves only a tooth-food-tooth phase consisting of a series of orthal retractions of the lower jaws. This corresponds to the tooth-food-tooth phase of mastication described by Crompton and Hiiemäe (1970) in the opossum. Presumably the most powerful biting occurs during this phase. The following tooth-tooth contact phase of mastication, generally involving transverse movements rather than orthal retraction of the mandible, occurs after the food has already been partially reduced. During the tooth-tooth contact phase of mastication, a large occlusal area is more important than a powerful bite.

The temporalis and mandibular adductor muscles of mammals and reptiles are not the only muscles involved in producing bite force. Other adductor muscles (for example, the masseter and medial pterygoid muscles in man) are not aligned with any bite point; their force of contraction is divided between useful bite force and wasted reaction force at the jaw joint.

Translatory freedom in jaw joints, together with alignment of bite point and muscle fibers, results in a high mechanical efficiency of the temporalis or mandibular adductor muscles in producing bite force. Any study of the mechanics of vertebrate jaw adduction must consider the morphology and action of the jaw articulations as well as the placement and orientation of the muscles.

CONCLUSIONS

Fore-aft translatory freedom is present in the jaw articulations of most vertebrates. This freedom is provided either by a sliding jaw joint or by a two-jointed jaw suspension. The most powerful muscles adducting the jaws are aligned with potential bite points along the tooth row. Translatory freedom of the jaw joint allows precise alignment of muscle force and bite point and reduces force wasted as reaction force at the jaw joint. During powerful biting the jaw is functionally a link between the muscle force and the bite force rather than a lever.

ACKNOWLEDGMENTS

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