Introduction

A number of simple mechanical models are used to analyze the mammalian masticatory apparatus. Beginning with an elementary two-dimensional lever system, additional equally simple models are used to explain basic structural features (the natural design) of the generalized mammalian jaw mechanism. Typically, a single feature of the jaw mechanism is emphasized in each study because its presence in many or most members of a group suggests that such a feature is important functionally. Using a simple model, the best possible configuration for the subsystem that includes the feature is then determined, consistent with the actual conditions in real animals. These models attempt to capture major features of the jaw mechanism rather than the finer details.

More details emerge as additional simple models are considered, but the main features remain paramount. Two major results of studies like this are that: (1) almost all mammalian jaw mechanisms have essentially the same *basic* structure; and (2) this approach has provided a general mechanical explanation for this basic structure. The finding that basic parts of the jaw mechanism are in some sense optimized makes it virtually inevitable that the most basic masticatory apparatus, found in the majority of mammalian groups, will be very similar. One probable reason that such similarities in the skulls and jaws of mammals are not more obvious is that the more superficial structural diversity of mammalian skulls and jaws is impressive and tends to mask the similarities in the more basic features.

Clearly, the overall structure of the mammalian jaw mechanism is extremely diverse. Best known, perhaps, is the diversity of the teeth. Although tooth loss is very common in mammals, the different kinds of teeth are positioned in essentially the same relative locations along the jaw.

The range in the shapes of the jaw itself is also noteworthy, but a basic structure is evident at the outset: joint at the rear, teeth at the front, and muscles in between.

Although their size and orientation are different in different animals, the same large muscles close the jaw. Moreover, they generally attach at equivalent places on the skull and jaw. In a few cases essentially a single muscle mass closes the jaw. Here, distinct muscles are difficult to discern.

The upper part of the jaw joint on the skull, the glenoid, is typically located above the general level of the tooth row. Only in a few cases, such as the fossil entelodonts, is the glenoid cavity on approximately the same level as the tooth row. Some saber-toothed cats may have had the glenoid below the row of teeth, but a number of different straight lines could theoretically be drawn from tooth to tooth so that a particular tooth "row" is difficult to determine. The condylar part of the jaw joint, on the lower jaw, is usually much more variable in position, and although often positioned some distance above the teeth it is just as often close to the same level as the tooth row.

The lower jaw of most mammals is a bar of bone that is often L-shaped, with the jaw joint on one end. The teeth fill a region at the other end of the jaw, and the resultant muscle force provided by the jaw muscles is located somewhere in between. This location of the muscle force in front of, or anterior to, the jaw joint has some significance. In this location the jaw closes when the muscles contract (it would open if the muscle force were located behind the joint).

Two other less obvious similarities seem important. First, there is virtually always a region of some length that is devoid of teeth and is located between the most posterior tooth and the jaw joint. Second, the different parts of the large jaw-closing muscles, while their size and action lines differ, tend to be attached more posteriorly along the jaw. Therefore, if the forces exerted by the individual muscles are imagined to be resolved into a single resultant force, this resultant appears to be located at a point within the posterior half, or even within the posterior third, of the jaw. Even in the case of many rodents, in which some *parts* of the muscle mass that closes the jaw attach rather far forward, the idealized *resultant* muscle force is located closer to the rear of the jaw. The almost universal presence of these two conditions in mammals implies a functional importance within the structure of the masticatory apparatus.

Finally, two other extremely important restrictions on the jaw mechanism are accepted for simplicity. First, maximum, rather than lesser, bite forces are assumed throughout because extreme cases are likely to be the most important. Second, the only biting situation considered in these studies is when the cheek teeth are occluded. That is, when the upper and lower teeth are touching, or (if some food is positioned between the teeth) almost touching.

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More information

1 The jaw viewed as a two-dimensional lever

An extremely simple and idealized two-dimensional model introduces this study of the natural design of the mammalian masticatory apparatus. The model treats the jaw as a lever with joint forces at one end, the output or bite forces at and near the opposite end, and the input muscle force somewhere in the middle. Results are constantly compared with the condition in real animals. The major result is that all the teeth will be located in front of the line-of-action of the imagined resultant force of the jaw muscles. The next two results are closely related. First, the line-of-action of the imagined resultant muscle force will be located about one-third of the jaw length from the jaw joint. Second, this location maximizes the sum of the bite forces along the entire length of the tooth row.

The location of the line-of-action is critical, because if the idealized moment arm of the muscles is fixed, then the lever system is also fixed. Bite forces then are determined only by the amount of muscle tissue available.

1.1 Location of the muscle force

At the outset, the importance of bite force to an animal is assumed. Certainly jaws perform many functions, but surely applying force to disrupt food items is one of the most important. As a first approximation, the production of a maximum bite force is an attractive idea. By itself however, it fails to explain the structure of the jaws. As will be seen, only *after* considering the forces at the jaw joint can one return to the idea of a maximum bite force; certain potential problems at the joint must first be avoided.

One way to begin an examination of how mammalian jaws work is to simplify the mechanism of the jaw in order to consider it as a two-dimensional structure and view the lower jaw from the side (Fig. 1.1). In this view, the teeth are attached at the anterior upper edge of the long, more-or-less horizontal, part of the jaw. Behind the teeth, it is usually possible to see three distinct regions of the jaw. First, behind and above the most posterior tooth, a pointed, and often curved, coronoid process serves as much of the site of attachment for the **temporalis** muscle, one of the three great muscles that close the jaw. Behind and below the coronoid is the second region, the articular process. On the end of this process is an articular surface that

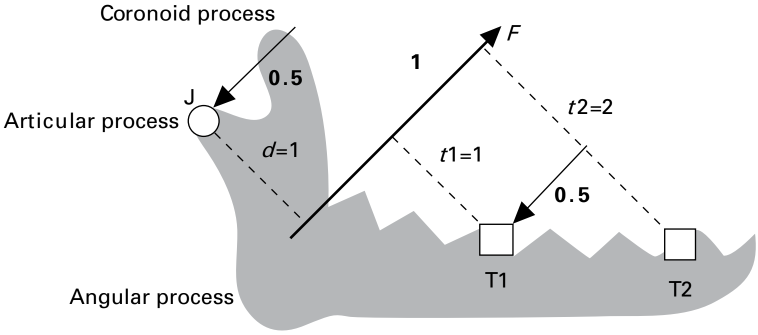

Figure 1.1. The circle (J) represents the jaw joint and the two squares, labeled T1 ad T2, indicate just two of the many teeth in the jaw. The arrow (*F*) is the resultant unit vector of jaw muscle force. The distance from the jaw joint to *F* is indicated by *d*. The distances *t*1 and *t*2 extend from the vector to their respective teeth. Note that all distances are perpendicular to the muscle force vector. The muscle force is 1 unit and the reaction forces (short arrows) at the joint and T1 are each 0.5 units.

forms the lower half of the jaw joint. The angular process (the third region, which in some cases may not be very prominent) forms the rear, lower corner of the jaw and serves as the attachment site for the two remaining large jaw-closing muscles. Much of the **masseter** attaches on the outer or lateral side and part of the **medial pterygoid** attaches to the inner or medial side of this angular process.

In Figure 1.1 the outline of a generalized jaw is indicated in silhouette and only the jaw joint and two representative teeth have been highlighted with symbols (circle and squares, respectively). In addition to the joint and the teeth, the other element needed for the following discussion is the force that is put into the system and that pulls the upper and lower jaws together. Most of this force is provided by the three great jaw-closing muscles already mentioned: temporalis, masseter, and medial pterygoid. The force provided by these three muscles, taken together, is represented by the arrow (**F**) that points up and toward the front of the jaw in this example (Fig. 1.1).

Thus, the arrow, or the resultant unit vector of jaw muscle force stands for the sum of all the forces provided by the many different parts of each of these three large muscles and is imagined to be applied at a single point. The various parts of the muscles actually pull in a number of different directions, but the arrow is meant to represent the orientation of a single force that results when all of the forces, from all of the different parts of the muscles, are considered together. Stated in another way, imagine that all the jaw-elevating muscles are removed. Then, a single force, pulling in the direction of the arrow, would have the same effect as the entire muscle mass where all the parts were active. Of course, Figure 1.1 is a general example. To represent accurately the direction of the resultant in each different mammalian species, theoretically, would require a different drawing for each case. The remaining items in this figure will be discussed at length in the following sections.

1.2 Moments of force

A two-dimensional lever can be represented as a simple line that can rotate around a single point when it is pulled by forces. As the forces provided by the jaw muscles rotate the "bar" of the lower jaw around the jaw joint, the lower jaw, in lateral view, is easily viewed as a lever. Imagining the jaw as such a lever, although far too simple, directs our attention to some important relationships.

Most of us are intuitively familiar with the fact that the magnitude of a force is not the only thing that counts when rotating a structure around a pivot. Push a door at the doorknob, for example, and the door swings easily. Apply exactly the same force close to the hinge and the same door may not move at all. Or put differently, a door can be swung with a small force at, or near, the knob but it takes a larger force to move the same door, with the same ease, if it is pushed farther from the knob and closer to the hinge. Thus, in addition to the force that is applied, the other important variable is its distance from the point of rotation, or the fulcrum. Likewise in a jaw, the magnitude of the muscle force is only part of the story; the effective location of an idealized resultant force is also important.

A single number can be derived from the *magnitude* of a force and its *distance* from a fulcrum. Simply multiplying these two quantities together produces a product called the *moment* of the force. This product, or moment, is an expression of the strength of the tendency to rotate a lever around its fulcrum. If distance is measured in feet and force in pounds, then the moment is expressed in foot-pounds. In the examples below, specific units are dispensed with for the sake of simplicity.

Very often more than one force will act on a lever. If, say, two forces tend to rotate a lever in the same direction, two moments, one for each force, are involved and they simply are added together. If one force tends to rotate the lever in one direction while the other force rotates it in the opposite direction, two possibilities exist. In the first case, the smaller moment is subtracted from the larger. The lever rotates in the direction appropriate for the larger moment, but the effect is reduced by an amount equivalent to the smaller, opposite moment. The second case is the more interesting. Here the opposite moments are equal, and so the lever does not rotate in either direction. The lever is then said to be in equilibrium.

If the *moments* are equal (i.e. the lever is in equilibrium), the *forces* involved can be either equal or unequal. Obviously, equal forces require equal distances from the forces to the fulcrum, if the products of force and distance are to be equal. But if the forces are unequal, the distances from the forces to the fulcrum must also be unequal. Here, the larger force must be paired with the shorter distance and the smaller force with the longer distance in order for the moments to be equal. Thus, a small force can balance a large force if the large force is closer to the fulcrum and the small force is farther away. The products of force and distance ($F \times d$), that is the moments, rotating the lever in opposite directions, are equal in an equilibrium condition ($F_1 \times d_1 = F_2 \times d_2$), and the lever will not rotate in either direction around its fulcrum. An important corollary to note is that the *ratio* of the two forces will be equal to the *ratio* of the two distances, that is $F_1{:}F_2 = d_2{:}d_1$. In order to see clearly how these observations will clarify the workings of the jaw, Figure 1.1 can be examined in more detail.

In Figure 1.1, the circle labeled **J** represents the jaw joint and the two squares labeled **T1** and **T2** indicate just two of the many teeth in the jaw. The arrow (***F***) indicates the line-of-action of the muscle force, and its length indicates a force of one unit of magnitude. The arrow is thus a unit vector. The distance from the joint to ***F*** is indicated by ***d***. The distances ***t*1** and ***t*2** extend from the unit vector to the respective teeth. Note that all distances, as in levers in general, are perpendicular to the unit vector that represents the jaw muscle force.

All the individual jaw muscle forces taken together are expressed as a single resultant force. The moment of force closing the jaw is the product of the magnitude of this muscle force and its distance from the jaw joint, which serves as the fulcrum of the jaw. In Figure 1.1, this product is obtained by multiplying the magnitude of the muscle force (***F***) by the distance ***d***, which is the muscle force vector's distance from the jaw joint. This moment of the muscle force rotates the jaw counterclockwise in this example. The muscle force can be thought of as the input force, because it is the force that is put into the jaw mechanism by the jaw muscles.

In our deliberately simplified example, the distance from the jaw joint to the idealized muscle vector is taken to be ***d***. For ease of calculation, assume that ***d*** is equal to one unit of distance. A muscle force of one unit of force also can be imagined (giving a unit vector), as we are only interested in relative forces. The muscles in a given animal do exert a force with a particular magnitude, but using a number other than 1 complicates the arithmetic without increasing our insight into how the mechanism of the jaw works. To determine the moment of the muscle force, we simply multiply this force (one unit of force) by its distance from the joint (one unit of distance). The counterclockwise moment of muscle force ($F \times d$) is therefore $1 \times 1 = 1$ (again, ignoring what the units of force and distance may actually be in any specific example). How the muscle force compares with the forces at the teeth will be examined next.

1.3 Reaction forces

As the inferred muscle force (***F***) pulls the lower jaw up, the front of the jaw will eventually cease to move any farther because either the upper and lower teeth come into contact or food that is between the teeth is compressed to its limit. The back end of the jaw also tends to move up. The rear of the jaw does not actually move very far because the joint surface is essentially in contact with a fibro-cartilaginous disk that is itself in contact with the joint surface on the part of the skull that forms the upper part of the jaw joint. Thus, there are two *downward* reaction forces that resist the *upward* motion of the jaw. One is at some point along the tooth row, the bite point, and the other is at the jaw joint. They are "reaction" forces because they are reactions to the muscle force; if there were no muscle force there would be no force at the teeth or the joint. In this overly simplified example they are the only reaction forces considered, and so these two forces taken together must be equal to the muscle force because they exactly balance the muscle force. Thus, the upward pull of the muscles on the lower jaw is balanced by two downward pushes; one is a bite force at a tooth, or a few teeth, and the other is a joint force at the jaw joint.

At this point the *general* location of the muscle force can be considered in more detail. If jaw rotation takes place around the jaw joint, then any resultant muscle force passing behind the joint would open rather than close the jaw. A muscle force passing through the joint will naturally be a distance of zero from the joint. The moment of that force will then be 0 and the force will have no turning effect on the lower jaw. It will simply force the joint surfaces toward each other. In order to close the jaw, the muscle force must be located in front of the joint. It must be located a reasonable distance in front of the joint if the moment of force is to have a sufficiently large turning effect. What exactly that reasonable distance might be will be considered in a later section.

When the jaw muscles rotate the jaw around the jaw joint until upward motion ceases because the lower teeth come into contact with a food item or with the upper teeth, the two reaction forces come into play. Once again, if there were no muscle force there would be no force at the teeth or the joints. As the jaw has stopped moving, it is in equilibrium. A jaw in equilibrium can be conceptualized as a bar that has a moment of muscle force rotating it counterclockwise around a fulcrum and an equal, and therefore balancing, moment of reaction force rotating it clockwise (Fig. 1.1). The upward muscle force that rotates the jaw in a counterclockwise direction is the *input* force. The downward reaction force at the bite point is the *output* force. The force at the joint is not rotating the jaw in either direction and will be considered later.

Assume that all the moments are equal when biting on a particular tooth – **T1**, say. The distance from the joint to the tooth is the sum of the distance from the joint to the idealized muscle force (***d***) plus the distance from the muscle force to the tooth (***t*1**). Imagine that ***t*1** is equal to ***d*** and both equal one unit of distance, so that the total distance from the joint to **T1** is two units, or twice the distance from the joint to the muscle vector. If we assume that the muscle force ***F*** is equal to 1, the counterclockwise moment of *muscle* force is equal to 1 ($1 \times 1 = 1$). Therefore, in order to be in equilibrium the clockwise moment must also be equal to 1. As the distance from the joint to the tooth is 2, the output force at the tooth must be 0.5 because 2×0.5 equals a moment of 1 (Fig. 1.1). Here we can recall the example of the door that was given earlier. In this case the muscle force is twice as large as the tooth, or bite force, but these forces have the same, although opposite, rotational effect because the large muscle force is one unit from the jaw joint while the small tooth force is two units from this joint. The two moments, or products of force and distance, 1×1 and 2×0.5, are both equal to 1.

Tooth **T2** provides an additional example. The distance from the jaw joint to this tooth is three units. This can be seen in Figure 1.1, where **T2** is two units from the muscle vector and therefore three units from the jaw joint (***d* + *t*2**). Recall that distance is always measured perpendicular to the vector. The moment of the *muscle* force remains 1, so the moment of the tooth or bite force must also be 1 when the system remains in equilibrium. Because the distance from the jaw joint to the tooth is three units, the tooth force at **T2**, multiplied by 3, must equal 1. Therefore, the tooth force (or output force) in this case is 0.33.

The magnitude of the muscle force is equal to one unit of force and the bite force at **T1** is equal to 0.5 (Fig. 1.1). The upward (counterclockwise) force is greater than the downward (clockwise) force, but the jaw does not rotate, because the moments are equal. At the same time, the entire jaw does not translate directly up toward the skull either, even though the muscle force pulling up is larger than the bite force pushing down. This is true because there is another force in the system.

There are only two places where the lower jaw contacts the skull in this model: the bite point and the jaw joint. Thus, the other half-unit of reaction force is found at the jaw joint. The jaw is not moving in two senses. First, it is not rotating around the jaw joint, because the moments of force are equal. Second, it is not moving straight up as a unit (translating), because the upward muscle force of one unit is balanced by *two* downward reaction forces of a half unit each: one at the bite point and the other at the jaw joint. Essentially the same can be said when biting at tooth **T2** (Fig. 1.1). Here, the reaction forces are not the same as they were when biting on tooth **T1**. Now they are 0.33 at the bite point and necessarily 0.66 at the jaw joint.

Unlike the bite forces at the teeth, however, the joint force is not doing the useful work of the jaw, such as crushing or slicing food, and is in a sense "wasted effort." One might expect that the joint force would be very small if that were possible; the smaller the amount of force dissipated at the joint, the more muscle force that is being used productively at the teeth. However, in mammals the joint force usually has a significant magnitude. There is an important reason for the presence of this joint force, which will be considered in some detail in a later section.

The idealized muscle force vector in this example is oriented up and toward the front of the jaw (Fig. 1.1). This anterior orientation was chosen simply as an example. In this diagram, there is no special significance to an anteriorly oriented, as opposed to a posteriorly oriented, vector. In Figure 1.2 the vector points up and toward the rear of the jaw. The muscle force is again equal to one unit. The vector's distance from the joint, one unit, is the same as the analogous distance in Figure 1.1. The distances from the jaw joint out to the respective teeth are also the same, and therefore, with a muscle force of one unit, the output tooth forces at **T1** and **T2** are also the same: 0.5 and 0.33 when the system is in equilibrium.

The muscle force is posteriorly oriented in most of the great groups of mammals. It is anteriorly oriented in only a few mammalian groups, although there are a large number of species in these groups. This is an extremely important point that will also be considered in greater detail in Chapter 3.

A solid line connects tooth **T1** and tooth **T2**, and extends to the rear as far as the jaw joint (Fig. 1.2). A perpendicular (***h***) has been dropped from the jaw joint to this line. This exercise clearly demonstrates that the jaw joint is located some distance (***h*** units) above the level of the tooth row. Even though it is often difficult or even

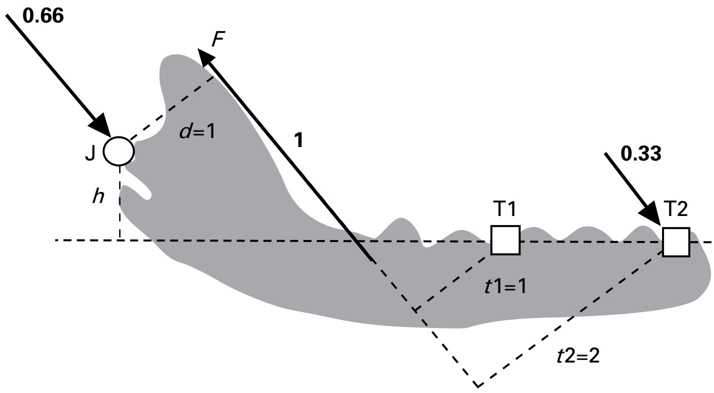

Figure 1.2. This figure represents a jaw with a posteriorly inclined muscle vector rather than one that is anteriorly inclined. The muscle force is 1 unit and the reaction force is 0.66 units at the joint and 0.33 units at the tooth T2. The other labels are as in Figure 1.1.

impossible to draw a straight line through a given tooth row, a joint that is above the general level of the tooth row is typical in mammals. The upper part of the jaw joint (on the skull) is almost always above the level of the tooth row. The lower part of the joint (on the lower jaw) is more variable. The same relationship can also be seen in Figure 1.1. More rarely in mammals, the part of the joint on the skull is situated on, or even below, the level of the tooth row. The significance of this location for the jaw joint, above or below the tooth row, also will be considered in Chapter 3.

In Figures 1.1 and 1.2, the output bite forces at two sample tooth positions were examined. The tooth farther away from the jaw joint exerts a lower output force than the tooth closer to the joint. This is true because as the distance from the joint to the tooth increases, the bite force must decrease if the moment of the bite force is to remain equal to the moment of muscle force.

1.4 Bite force along the tooth row

The previous elementary analyses can be expanded to include a larger number of output bite forces located all along a simple two-dimensional jaw. The same simple calculations that were used above can be used to determine the output force at any number of bite locations along a jaw (bite force is equal to the distance, say 3, from the joint to the vector multiplied by the muscle force of one unit divided by the distance from the joint to the bite point, that is $y = 3/x$). These forces can then be plotted on a graph to give a visual impression of output bite force at different locations along a potential tooth row (Fig. 1.3). On such a graph, bite force is indicated on the vertical axis. Locations along the jaw are marked on the horizontal axis, from the jaw joint, at the left at 0, all the way out to the right-hand side at location 10, where the anterior incisor tooth is located. To simplify the following examples as much as possible, the jaw will be represented as a straight, horizontal line. The

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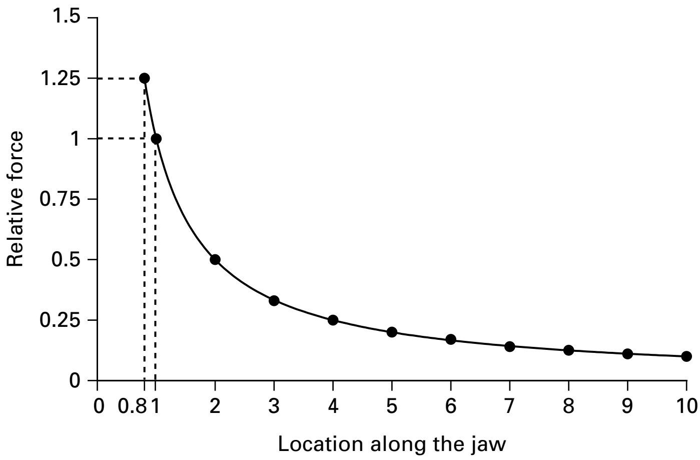

Figure 1.3. A plot of relative bite force against location along a jaw ten units long. The jaw joint is positioned at location 0 and the 1 unit of muscle force is positioned at location 1 in this example.

joint is located at one end, the teeth fill a region of variable length at the other end, and the muscle force is located somewhere in the middle. As another simplification, the resultant muscle force is oriented at right angles to the line representing the jaw; in fact it would usually have a posterior or an anterior inclination in a real animal. Recall that the vector of muscle force must be located at least some distance in front of the joint if contraction of the muscles is to close the jaw. If the vector of muscle force were located behind the jaw joint, the jaw would open, rather than close, when the muscles shortened. If the muscle force vector passed directly through the jaw joint, it would neither open nor close the jaw.

The actual location of the vector of jaw muscle force has only been estimated and has yet to be measured with a great deal of accuracy in a real animal, although a later theoretical analysis, in section 3.6 in Chapter 3, attempts to predict this location. In any event, to see the effect of the idealized location of the muscle force along the jaw, a hypothetical location for a unit vector, say, location 1 can be chosen for consideration. As already mentioned, calculated bite forces at locations closer to the jaw joint are higher than forces at locations that are farther away from the joint. The graph is a smooth curve that slopes down toward the anterior end of the jaw at the right (Fig. 1.3).

In the particular example in Figure 1.3 a force of one unit is assumed for the muscle vector because we are, again, interested only in relative bite forces. Moreover, the assumption is that the muscle vector is applied at location 1. Therefore, the tooth that is also at location 1 will exert a bite force of one unit. In addition, at all potential bite locations that are anterior to the muscle vector and thus farther from the joint, the bite force is lower than the muscle force. This is necessarily true because longer distances to a tooth require correspondingly lower bite forces if a constant moment is to be maintained (recall that an equilibrium condition is