Jaw muscle size and bite force magnitude in relation to craniofacial morphology

Raadsheer, M.C.

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CHAPTER 2 HETEROGENEITY OF FIBER AND SARCOMERE LENGTH IN THE HUMAN MASSETER MUSCLE

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Abstract - This study deals with regional differences in the architectural design of the human masseter muscle. For a number of defined muscle regions the three-dimensional coordinates of origin and insertion points, and the lengths of the muscle fibers and sarcomeres were determined in the closed jaw position. Measurements were made from cadavers and the data were used as input for a model predicting sarcomere length at other mandibular positions. At a closed jaw average muscle fiber length of the muscle regions ranged between 19.0-30.3 mm. The fibers appeared to be considerably longer (35%) anteriorly than posteriorly in the muscle, and deeply situated fibers were on average 5% shorter than superficially situated ones. Average sarcomere length of the regions ranged between 2.27-2.55 μm, indicating that at a closed jaw position sarcomeres are at suboptimum length and have different positions on the length-tension curve. In the deep layer of the muscle sarcomeres were significantly shorter (6%) than in the superficial layer. Within the superficial layer sarcomere lengths did not differ significantly, but in the deep layer sarcomeres were shorter (8%) posteriorly than anteriorly in the muscle. The model shows that jaw displacement had a different effect on sarcomere length in the muscle regions. When the jaw was rotated about a transverse axis (open/close rotation) sarcomere excursions were relatively small in the posterior muscle regions and large in the anterior regions. The reverse was true when the jaw was rotated contralaterally about a vertical axis. It is concluded that, due to heterogeneity in fiber and sarcomere lengths, the distribution of maximal isometric tension across the muscle at full effort is not uniform.

2.1 INTRODUCTION

Knowledge of the architectural design of a muscle is important in understanding its functional capabilities. It is well known that the force a muscle can produce depends on the length and the shortening velocity of the sarcomeres and that the proportion of origin-insertion distance occupied by contractile tissue affects the occurring length changes. The longer a muscle fiber, the larger the number of sarcomeres in series and thus the smaller is the length change per sarcomere. Especially in the last decade our insight into the functional consequences of muscle architecture has increased considerably (a.o. Muhl, 1982; Woittiez *et al.*, 1983; Huijing, 1985; Cutts, 1988). These studies were mostly concerned with the overall effects of architecture, *i.e.*, muscles were treated as homogeneous structures applying force to the skeleton via single, circumscrip tendon.
The human masseter muscle, however, is irregularly shaped and has relatively broad attachment areas. Within the muscle regional differences exist in spatial orientation and position of muscle portions relative to the jaw-joint and their origin-insertion lengths vary across the muscle. Hence, it can be expected that during jaw movements muscle fiber and sarcomere excursions are not the same for various muscle regions, and this has been demonstrated in the masseter muscle of the rat (Nordstrom et al., 1974), the pig (Herring et al., 1979), and the rabbit (Weijis and Van der Wielen-Drent, 1983).

In the present study the fiber and sarcomere lengths for a number of defined muscle regions in the human masseter muscle was investigated for the closed jaw position. In addition, the spatial coordinates of attachment points were determined, allowing to predict sarcomere length changes in these regions during a number of defined jaw movements. This way it was possible to relate our morphological findings to potential functional consequences.

2.2 MATERIALS AND METHODS

2.2.1 Materials
Eight fresh cadavers (four male, four female), Caucasians, age: 78.3 ± 9.2 years (mean ± SD) were used to take samples from the right masseter muscle. Dissection was carried out within 24 hours after death. The mouth of the cadavers was closed and the jaws were edentulous. The upper and lower prostheses were left in situ. Prior to dissection, metal plates were connected to maxilla and mandible in the incisal region in order to prevent relative movements of the jaws.

2.2.2 Sampling of muscle portions
After the muscle was freed from overlying tissue, six muscle portions were carefully dissected. Traditionally, the masseter muscle is subdivided into a superficial and deep layer. Of each of these two layers, an anteriormost, intermediate, and posteriormost portion was obtained for measurements; each portion had a diameter of about 0.5 cm. The portions were defined as follows: 1) The anteriormost superficial portion constitutes the anterior rim of the muscle, arising from the zygomatic bone and inserting just above the lower margin of the mandible, about 1.5 cm anteriorly to the angulus mandibulae. 2) The intermediate superficial portion arises halfway the origin of the superficial layer from the zygomatic arch and inserts near the angulus. 3) The posteriormost superficial portion forms the posterior margin of the superficial layer; it originates from the zygomatic arch and inserts onto the posterior margin of the mandibular ramus, approximately 1 cm above the angulus. 4) The anteriormost and 5) intermediate deep portions lie directly deep to 1) and 2), with which they share their origin; the fibers insert onto the lateral surface of the mandible, about 1.5 cm cranially to the lower mandibular margin. 6) The posteriormost deep portion is not covered by the superficial layer of the muscle; it takes
origin from the posterior third of the zygomatic arch and inserts onto the lateral side of the ramus, about 1 cm anteriorly to the posterior margin and 1.5 cm above the angulus.

Prior to removal, ties were placed around the ends of each portion, at the sites of attachment onto the bone. The distance between the ties (i.e., the origin-insertion length) was measured to the nearest millimeter by means of calipers. The average length of the contractile part (we will call this muscle fiber length) was determined by measuring the distance between the estimated centroids of attachment of the fibers to the tendon or to the bone. After excision the portion was fixed to a spatula, keeping the origin-insertion length at the value measured in situ, and placed in fresh fixative.

To register the spatial coordinates of origins and insertions in the cadaver, the centroids of areas of attachment were marked by steel balls (diameter: 1.0 mm) glued into the bone surfaces. Two perpendicular radiographs were taken according to the method described by Koolstra et al. (1988). The coordinates were defined relative to a Cartesian coordinate system. The origin was centered between the two joints, the x- and y-axes were parallel to the Frankfort Horizontal plane and were pointing, respectively, anteriorly and laterally; the z-axis was perpendicular to that plane.

2.2.3 Sarcomere length measurements
The muscle samples were fixed for 1 week in a solution of 4.8% alcohol, 6.8% formaldehyde, 0.16% fenol, 5% chloral hydrate, 3% sal carolinum, and 3% glycerine. Subsequently they were macerated (1 week) in 6% H$_2$SO$_4$ and stored in a 50% solution of glycerol. From each muscle portion six small fiber bundles, approximately one fiber thick with several fibers lying side by side, were randomly teased out under a dissection microscope. Of each bundle the length was measured to the nearest millimeter. Then the bundles were mounted on a microscope slide in glycerine jelly. In each bundle one intact fiber was chosen to determine sarcomere length. At six equidistant locations between the ends of the fiber the number of sarcomeres was counted along a length of 100 μm/location at a magnification of x 1,000 using a Zeiss microscope with a micrometer eyepiece.

2.2.4 Prediction of sarcomere length for different mandibular positions
Of each muscle portion average sarcomere length, fiber length, and the three-dimensional coordinates were measured for the closed jaw. For all other mandibular positions sarcomere length can be calculated from the changed distance between origin and insertion with respect to the initial position by using the model described earlier by our group (Weijs et al., 1987). The pinnation angle of the muscle was estimated to be 20% on the average. As the three-dimensional displacement of insertion points of the muscle are not known for normal activities (e.g., chewing), open/close excursions and laterodeviations were chosen as characteristic rotations of the jaw. Prediction of sarcomere length was carried out for the following six rotations, each with
a range of 30°, in 1° increments. Rotation in the sagittal plane: 1) about a transverse axis running through the temporomandibular joint ("hinge axis") and 2) about a transverse axis situated 2.5 cm below the joint, i.e., halfway the mandibular ramus. Laterodeviations of the closed jaw: 3) to the right (ipsilateral) side about a vertical axis situated in the right joint and 4) to the left (contralateral) side about a vertical axis situated in the left joint. Laterodeviation combined with jaw opening [5) and 6)]: these movements are similar to 3) and 4), but now each degree of laterodeviation is accompanied with a jaw opening of 0.5° about a transverse axis, halfway the ramus.

2.3 RESULTS

2.3.1 Muscle fiber length
To examine whether teasing of bundles of fibers affects fiber length, the length of each muscle portion, measured in situ, was compared with the average length of the six bundles teased out of the portion. Absolute differences in fiber length ranged between 0-8 mm (mean ± SD: 2.6 ± 2.8 mm, n=48: 8 subjects x 6 portions). A paired Student’s t-test demonstrated that the difference was not statistically significant (p<0.05). The variability of muscle fiber length within a muscle portion, as estimated by the coefficient of variation (CV=SD/X * 100%), ranged between 0.1-18.9% (mean ± SD: 6.4 ± 4.3%, n=48). One-way analysis of variance revealed that this variability did not differ significantly (p<0.05) between the six muscle portions.

Figure 1 shows fiber length (for each subject average value of the six fiber bundles was used) and tendon length (calculated by subtracting fiber length from origin-insertion length) in the six muscle portions; the standard deviation values are a measure for interindividual variability. There appeared to be a clear heterogeneity in fiber length within the muscle. The average length ranged between 19.0-30.3 mm. Fibers in the posteriormost portions were about 36% shorter than those in the anteriormost portions, and, although less obvious, in the deep layer of the muscle they were on average 5% shorter than in the superficial layer. Paired Student’s t-tests were used to survey for differences within and between the two layers of the muscle. Two within-layer comparisons (i.e., anteriormost vs. intermediate and intermediate vs. posteriormost portions) and three between-layer comparisons (i.e., anteriormost superficial vs. anteriormost deep, intermediate superficial vs. intermediate deep, and posteriormost superficial vs. posteriormost deep) were carried out. It was found that the anteriormost superficial portion did not differ significantly (p<0.05) from the intermediate superficial and the anteriormost deep portions. In contrast, the other five comparisons yielded a significant (p<0.05) difference in fiber length.

With respect to tendon length the same mutual comparisons were carried out. Within the superficial layer of the muscle tendon length did not differ significantly between the portions. In
the deep layer there was no significant difference between the anteriormost and intermediate portion, but the tendon of the posteriormost portion was significantly (p<0.05) shorter than that of the intermediate portion. All three between-layer comparisons yielded significant (p<0.05) differences, the tendons of the deep layer being on average 35% shorter than those of the superficial layer.

As can be seen in Fig. 1 the distance between origin and insertion decreases going from anterior to posterior and from superficial to deep in the muscle. The results of the above-described comparisons indicate that the anterior-posterior decrease is primarily associated with a decrease in fiber length and the superficial-deep decrease with a decrease in tendon length.

2.3.2 Sarcomere length
For each fiber six sarcomere length values were available and within-fiber variability was estimated by the coefficient of variation. It appeared that the within-fiber variability ranged
between 1.1-14.6% (mean ± SD: 7.1 ± 3.1%, n=288: 6 fibers x 6 portions x 8 subjects). The variability in sarcomere length between the fibers of a muscle portion was estimated by the coefficient of variation value of the six (i.e., number of fibers/muscle portion) mean fiber sarcomere lengths. It ranged between 3.6-11.8% (mean ± SD: 6.8 ± 1.8%, n=48: 6 portions x 8 subjects).

For each muscle portion, grand means of sarcomere length were used to compute average sarcomere length of the eight subjects (see Fig. 2); the SD values in this Figure are an estimate of interindividual variability in sarcomere length. Average sarcomere length of the portions ranged between 2.27-2.55 μm. Sarcomeres in the deep layer of the muscle were on average 5% shorter than those in the superficial layer. Mutual comparisons of sarcomere length revealed that in the posterior and intermediate region of the muscle deeply situated sarcomeres were significantly (p<0.05) shorter (6%) than superficially situated ones; anteriorly there was no significant difference between the two layers. Comparisons of sarcomere length within the superficial layer did not show any significant difference between the three portions. In the deep

![Fig. 2. Sarcomere length in different portions of the masseter muscle.](image_url)
Fig. 3. The action lines of the muscle portions projected in the sagittal (A: lateral view) and transversal (B: cranial view) plane. Continuous lines, closed position; dashed lines in lateral view, position of action lines of the antiromost and posteriormost muscle portion after opening of the jaw about a transverse axis situated halfway the ramus (□); dotted lines, displacement arcs of insertion points; dashed lines in cranial view, action lines of these muscle portions after contralateral deviation about a vertical axis located in the left joint (▲). ■, Position of transverse axis situated in the joint; △, vertical axis situated in the right joint.
Table 1. Coordinates (mm) of origin (O) and insertion (I) of the six muscle portions

<table>
<thead>
<tr>
<th></th>
<th>x'</th>
<th>y'</th>
<th>z'</th>
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</thead>
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<tr>
<td></td>
<td>O</td>
<td>I</td>
<td>O</td>
</tr>
<tr>
<td>Superf. anterior</td>
<td>52.7 ± 3.2</td>
<td>15.3 ± 9.1</td>
<td>40.5 ± 4.6</td>
</tr>
<tr>
<td>Superf. intermediate</td>
<td>44.5 ± 3.7</td>
<td>0.4 ± 5.6</td>
<td>51.5 ± 5.1</td>
</tr>
<tr>
<td>Superf. posterior</td>
<td>34.0 ± 3.6</td>
<td>0.7 ± 6.0</td>
<td>56.5 ± 5.9</td>
</tr>
<tr>
<td>Deep anterior</td>
<td>54.8 ± 3.4</td>
<td>18.2 ± 4.0</td>
<td>40.5 ± 4.6</td>
</tr>
<tr>
<td>Deep intermediate</td>
<td>44.5 ± 3.7</td>
<td>12.0 ± 6.7</td>
<td>51.3 ± 5.1</td>
</tr>
<tr>
<td>Deep posterior</td>
<td>21.9 ± 3.3</td>
<td>9.1 ± 3.0</td>
<td>60.6 ± 5.4</td>
</tr>
</tbody>
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1Positive x-, y- and z-axes are pointing, respectively, anterior, right, and upwards.

layer, however, the sarcomeres in the posterior portion were significantly (p<0.05) shorter (about 8%) than those in the intermediate portion, but there was no significant difference between anterior and intermediate portions.

2.3.3 Predicted sarcomere length changes

For the model simulations the average values of sarcomere length, fiber length, and coordinates of origin and insertion (Table 1) at the closed jaw position were used as input data. Results will be described for the anteriormost superficial and posteriormost deep portions of the muscle. Changes in sarcomere length in the other four portions were generally found to lie in between these extreme cases.

The effect of a particular movement on sarcomere length changes depends on two factors. Firstly, the longer the muscle fiber, the smaller the induced length change per sarcomere. Secondly, the perpendicular distance between the axis of rotation and the muscle portion’s action line, i.e., the moment arm, determines the amount of length change between origin and insertion, a long moment arm producing a larger displacement of the insertion than a short moment arm. This is illustrated in Fig. 3 for the projections of attachment points in the sagittal and transverse planes, averaged over the eight subjects. During jaw opening (see lateral view, Fig. 3) the increase of origin-insertion distance is larger anteriorly than posteriorly in the muscle. In addition, if the opening movement occurs about a transverse axis situated in the joint the excursion of the muscle portions is larger than in the case that the axis is situated halfway the ramus (not shown in Fig. 3). These differences are clearly reflected in the amount of predicted sarcomere lengthening (Fig. 4). For the jaw opening about the joint axis sarcomeres are extended from about 2.5-4.8 μm in the anteriormost portion and from 2.3-3.5 μm in the posteriormost portion; in the case of a more caudally located opening axis these figures are 2.5-4.0 μm and 2.3-3.5 μm, respectively. In comparing the amount of sarcomere lengthening in the two muscle portions, it should be realized that muscle fibers in the anteriormost portion were found to be longer than those in the posteriormost portion. If this had not been the case, the
Fig. 4. Predicted sarcomere length changes in the anteriormost (A) and posteriormost (B) muscle portions for different jaw displacements from the initial closed position. i-lateral, ipsilateral deviation; c-lateral, contralateral deviation.
amount of predicted sarcomere extension in the anteriormost portion would even have been larger.

When from the initial position the closed jaw is moved to the right side (ipsilateral deviation) about a vertical axis situated in the right joint, there is but a slight increase of origin-insertion distance and the increase is larger for the anteriormost than for the posteriormost portion. Nevertheless, in both portions sarcomere extension is the same (about 0.1 μm). This is because of the longer muscle fibers in the anteriormost portion. Obviously, ipsilateral laterodeviation combined with jaw opening leads to an additional increase of sarcomere lengthening, the effect of opening being larger anteriorly in the muscle than posteriorly.

When the jaw is moved to the left side (contralateral deviation, see cranial view, Fig. 3) about a vertical axis in the left joint the occurring sarcomere length changes are more complex. Excursions are relatively small (from 2.5-1.8 μm) in the anteriormost portion and large (from 2.3-4.0 μm) in the posteriormost portion (Fig. 4). Insertions of the muscle portions move anteriorly and medially. Initially they are located posteriorly of their corresponding origin points, later anteriorly. As a result sarcomeres shorten initially, but start to lengthen as the movement continues. The tilt of a muscle portion’s action line relative to the vertical determines the lateral excursion angle at which this transition between shortening and lengthening takes place. The larger the tilt, the larger this angle. For this reason in the anteriormost muscle portion shortening of sarcomeres occurs during the largest part of movement and in the posteriormost portion only during the first 5-10°.

2.4 DISCUSSION

The presented results demonstrate that the human masseter muscle has a heterogeneous architectural design. The internal structure of the muscle shows several gradual changes, both along the antero-posterior and lateral axes. It appeared that origin-insertion distance and fiber and sarcomere lengths are larger anterior and superficial in the muscle than, respectively, posterior and deep, although there were some exceptions. Studying the architecture in the human lower limb muscles, Wickiewicz et al. (1983) and Friederich and Brand (1990) found that within a given muscle fibers have similar lengths. Such constancy does not exist in the masseter muscle. Our data confirm and extend the measurements of Schumacher (1961), who also found an anteroposterior decrease in fiber length of about 30%.

The potential importance of the observed architectural differences for muscle function can be explained in terms of actual sarcomere length and the range of sarcomere length changes. The isometric force a muscle can generate depends on the length at which the sarcomeres are activated (length-tension relationship). As far as we are aware no experimental data are available on optimum sarcomere length (i.e., the length at which maximal isometric force is produced) of human muscles. Based on I-segment length-measurements in human leg muscle fibers, Walker
and Schrodt (1973) constructed a length-tension curve for human sarcomeres with an optimum length of 3 \( \mu \text{m} \). If this curve is used for the masseter muscle, then all muscle regions investigated in the present study are below optimum length in the closed jaw position. This parallels findings in the masseter muscle of the rat (Nordstrom et al., 1974), pig (Herring et al., 1979), and rabbit (Weijs and Van der Wielen-Drent, 1983). Recently, Anapol and Herring (1989) determined length-tension curves of the whole masseter muscle of the pig and they found that in the closed jaw position the muscle is at suboptimum length and produces about 80% of its maximum tension. The present results point to regional variation in sarcomere length, also described for the masseter of other mammals (Nordstrom et al., 1974; Herring et al., 1979; Weijs and Van der Wielen-Drent, 1983). Hence, given equal activation of muscle fibers, there are regional differences in produced tension. From the length-tension curve given by Walker and Schrodt (1973) it can be derived that at closed jaw tension ranges between about 80% (in the posteriormost region) and 90% (in the anteriormost region) of maximal tension. In the human increase of maximal bite force when the mouth is opened has been observed by Manns et al. (1979) and Mackenna and Turker (1983), also indicating that the jaw muscles are at suboptimum length with closed jaws.

The effect of jaw displacement upon sarcomere length varies between the muscle regions. This can be explained by differences in 1) moment arm length, 2) initial sarcomere length at the closed jaw, and 3) the number of sarcomeres in series. The farther away a muscle portion is from the rotation axis, the longer is its moment arm and the larger is the induced change of origin-insertion length. This change is absorbed by the sarcomeres (also by stretching of the series elastic and tendon elements, but this effect is neglected in the present study) and the larger the number of sarcomeres in series, the smaller is the length change per sarcomere relative to the initial length. Theoretically, equivalent change of sarcomere length, and consequently of tension, in the different muscle regions can be attained if the regions lie parallel and the ratio of sarcomere numbers is proportional to the ratio of moment arm lengths (Gans and De Vree, 1987). Obviously this is not the case in the human masseter muscle, neither for open/close movements, nor for laterodeviations or a combination of both (Fig. 4). For example, when the mouth is opened sarcomeres are stretched more anteriorly than posteriorly in the muscle. Although we found longer muscle fibers, and thus more sarcomeres, anteriorly than posteriorly in the muscle (sarcomere number ratio: 1.3/1.0), this is not enough to compensate for the longer moment arm of the anteriorly situated fibers (moment arm ratio: 2.5/1.0). It implies that for different open/close positions variation in tension is larger anteriorly than posteriorly in the muscle. The conclusion seems justified that during jaw displacements the distribution of tension across the muscle is not uniform but varies continuously due to differential stretching of sarcomeres. As a result not only the magnitude but also the orientation of the resultant muscle force vector is not constant. It has been shown earlier that a varying action line increases the mechanical potential of the muscle (Van Eijden et al., 1988). Except for regional differences in
sarcomere excursions, the orientation of a muscle’s action line can also be varied by differences in activation (Blanksma and Van Eijden, 1990). For the human masseter such a difference has been established by Belser and Hannam (1986), who used wire electrodes inserted superficially and deeply into the muscle. Thus far, however, in most studies on the functioning of the masticatory system the muscle has been treated as a single unit (a.o. Manns et al., 1979; Van Eijden et al., 1990).

This study indicates that for a proper analysis of the functioning of the masseter muscle, the muscle should properly be subdivided into a number of independent elements, each having its own architectural features. The present analysis is a first approach to such an analysis, but is still crude. Effects of regional differences in fiber angulation, histochemical muscle fiber type (Eriksson and Thornell, 1983), and of elasticity of series elastic and tendon elements have not been taken into account. Also, the simulated jaw displacements are arbitrary and have been restricted to main components of movement, not occurring in everyday life. In addition, this study does not answer the question why for example muscle fibers and sarcomeres have different initial lengths. Some reasonable explanations have been given for the masseter muscle of the rabbit (Weijs and Van der Wielen-Drent, 1983; Weijs et al., 1987) and pig (Herring et al., 1979), using a combination of various techniques such as electromyography (EMG) and description of architecture. A possible approach for the human masseter could be collection of architectural data in cadavers and registration of three-dimensional jaw displacements during natural movements (e.g., chewing) in vivo under simultaneous registration of EMG-activity of subpopulations of muscle fibers, using fine wire electrodes. The displacement data can then be used to predict sarcomere length changes in different muscle regions and to relate these changes to the observed activity patterns.

2.5 REFERENCES


