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A new model for calculating muscle forces from electromyograms

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Summary. A muscle model is described that uses electromyogram (EMG), muscle length and speed of contraction to predict muscle force. Physiological parameters are the Hill constants and the shape of the twitch reponse to a single stimulus. The model was incorporated in a jaw model of the rabbit and tested by predicting the bite force produced by the jaw muscles during mastication. The time course of the calculated force appeared to match the bite force, measured in vivo by a strain gauge, applied to the bone below the teeth. The variation in peak strain amplitude from cycle to cycle correlated with the variation predicted by the model. The peak amplitude of the integrated EMGs of individual jaw muscles showed an average correlation with peak strain of 0.41. Use of the sum of the available peak amplitudes, weighted according to their effect upon the bite force increased the correlation to 0.46; the model predicted bite forces showed a correlation of 0.57 with the strain. The increase in correlation was statistically significant. The muscle forces were calculated using a minimum number of easily obtainable constants.

Key words: Electromyography – Biomechanics – Mastication – Jaw muscles – Muscle models

Introduction

The electromyogram (EMG) is one of the few clues to the mechanical action of muscles in the intact body available to the investigator. The kinematics of body segments and the external forces exerted about joints are the net result of the actions of a varying number of agonists, and sometimes antagonists. In many areas of applied research where EMGs are used, for instance in orthopaedics, sports medicine and revalidation, it is essential not only to know the external but also the internal forces acting in a system. It is then necessary to estimate the mechanical output of individual muscles.

Since the work of Lippold (1952) and Inman et al. (1952) there has been considerable interest in the use of the EMG signal as a muscle force predictor (for review see Basmajian and de Luca 1985). Nevertheless, the belief is still widespread that this is not feasible (Ralston 1961). In the last decade, it has been demonstrated by different investigators that force prediction, within certain limits of accuracy, is possible (Hof and van den Berg 1981; Olney and Winter 1985; Otten 1987; Winters and Stark 1987; Dowling and Norman 1988). Most of the methods employ either calibration procedures, where parameter values are adjusted until predicted and observed forces match, or large numbers of literature-based physiological parameters. The purpose of this paper is to describe and test a newly developed model that needs no fitting procedures and uses a very small number of parameters. This muscle model is nested in a model of the masticatory apparatus (Weijs et al. 1987) of the rabbit, a system that highlights the problems of multi-muscle joint systems. Eight jaw closing muscles, each with its own peculiar position and architecture, act about two joints with degrees of freedom for open-close and transverse (side-to-side) rotation.

The starting point for all muscle models is a presumed relationship between the mean integrated EMG (iEMG) value and isometric tension. The second step taken in most models is the attribution of two properties to the contractile component of muscle, i.e. a spring property, namely the dependence of contractile force on the length of the muscle fibres and a viscous property, the dependence of force on the rate of length change. Finally, the complex linkages in time are modelled to describe the activation of the cell membrane and the building up and decay of force (active state) by the cross-bridges (excitation-contraction coupling) and between active state and external force.

Unfortunately, the interference EMG does not contain information which can be unequivocally interpreted as to:

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1. The number of motor units firing and their firing rates, because no distinction can be made between the few units firing at high rates or the many at low rates.
2. The relative participation of slow and fast motor units, with different force-velocity and excitation-contraction properties.

Therefore any model, regardless of its sophistication in mathematical procedures or use of physiological data at the cell level, will be relatively crude.

The basic parameter of the muscle model described here is the shape of the twitch response of the muscles under study. It has been assumed that the electrical activity of the muscle at any time is proportional to the number of muscle fibres recruited at that moment. The twitch response following their recruitment is the result of the excitation-contraction process and the shortening process of the contractile element at the expense of the series elastic element. Twitches can be recorded easily both from human and animal muscles. We have shown that a model based on the twitch response produces reliable results and can be used to study muscle participation in complex anatomical systems in man.

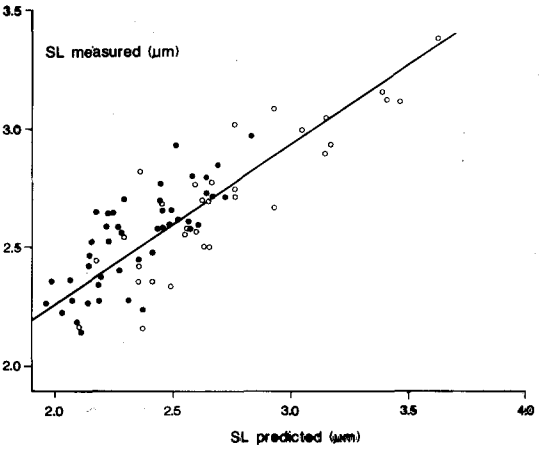

Fig. 1. Comparison of model predicted and histologically measured sarcomere lengths in 12 masseter muscle regions in seven different jaw positions. *Open symbols* refer to symmetric, *closed symbols* to asymmetric positions of the mandible. The sarcomere length (SL) measurements are means for five animals, the standard deviation is approximately 0.1 µm; the SL predictions are based on average morphological and movement data of Weijs et al. (1987, 1989b) taken from other individuals

Methods

Materials. Experiments were performed with adult male New Zealand domestic rabbits (*Oryctolagus cuniculus L.*) ranging in mass between 2–4 kg. The experimental protocol was approved by the University Board for Animal Experiments.

Jaw model. The jaw model has been described previously (Weijs et al. 1987). In this model the complete bilateral musculature is represented by 30 muscles, each modelled by one vector. The measured points of origin and insertion of the vectors determine the length of the muscle and the position and direction of the muscle force in space. The maximal force is determined by the total cross-sectional area of the muscle fibres, the actual force during chewing by the muscle model. Furthermore reaction forces are exerted at the two jaw joints and a bite point situated at the middle of the row of cheek teeth of the chewing side. Any movement of the jaw carries the muscle insertion points and the bite point to another location. The two points of application of the two joint forces are assumed to be fixed relative to the skull.

After determination of the force vector and moment vector of each muscle, the resultant force and moment vectors at the chewing and non-chewing side are calculated. Assuming fixed directions for the joint reaction forces in the sagittal plane, the bite force magnitude and direction can be calculated by solving the equations for static equilibrium.

Sarcomere length. When the jaw is closed, fibre length and sarcomere length (*SL*) are known (Weijs and van der Wielen-Drent 1982, 1983; Weijs et al. 1987). Jaw movements during mastication can be characterised by a changing angle of jaw opening and of lateral rotation about specific axes of rotation. These angles are known, for chewing three kinds of food, from a cineradiographic study (Weijs et al. 1989a, b). These studies and the one of Schwartz et al. (1989) have shown that the masticatory movements, with the exception of the first few and last few cycles, are quite stereotyped. Therefore, the mean movement profiles for mastication of pellets, hay or carrots were used to calculate muscle lengths and length changes.

The calculations of *SL* were carried out for the average jaw position in each of 20 equidistant intervals into which the chewing cycles had been divided. Assuming that the muscle is composed of fibres in series with an inextensible tendon, for all muscles, intervals and foods, the fibre length and an initial estimate of *SL* can now be calculated.

Available measurements of *SL* at 12 sites in the rabbit masseter muscle in seven jaw positions (Weijs and van der Wielen-Drent 1982) were used to check the initial estimates. The SL for a closed jaw was used as a starting point to calculate *SL* in the other six jaw positions. Figure 1 shows the model predicted (SL_{pr}) and measured sarcomere lengths (SL_m) for symmetric and asymmetric jaw positions.

For the symmetric jaw positions a regression equation

$$SL_m = 0.67\,SL_{pr} + 0.91 \quad (r = 0.83,\ n = 26) \tag{1}$$

is obtained (*SL* in µm), for the asymmetric positions a similar equation

$$SL_m = 0.64\,SL_{pr} + 1.03 \quad (r = 0.74,\ n = 51) \tag{2}$$

Both correlations are highly significant ($P < 0.001$). The slopes of the relationships are clearly below unity. In the final estimate of SL the values have been corrected by incorporation of the first of the two regression equations.

Muscle model. All input data (muscle length, length change, EMG) and output data (forces) were defined per interval. An interval lasted on average 13 ms. The force a muscle exerted in interval i (F_i) was equal to

$$F_i = F_{max} \cdot (FL_i \cdot FV_i \cdot FQ_i + FP_i) \tag{3}$$

where F_{max} is maximal tetanic force (30 $N \cdot cm^{-2}$ of cross-section); *FL* is force/length factor, dependent on the length of the sarcomeres; *FV* is force/velocity factor, dependent on the velocity of the sarcomeres; *FQ* is activation factor, dependent on the EMG level; *FP* is force scaling factor for the parallel elastic element. FL_i and FV_i depended on the average length and length change of the sarcomeres in interval i, respectively. The FQ_i depended on *iEMG* levels in interval i and previous intervals, as there was a delay between the electrical and mechanical activation of the muscle.

The force length factor (*FL*) was estimated by the following third degree equation fitting experimental data from rabbit digastric muscle (Muhl et al. 1978)

$$FL = 0.41\,SL^3 - 4.40\,SL^2 + 14.80\,SL - 15.05 \tag{4}$$

(*SL* in μm; negative values of *FL* are replaced by zeros, optimal *SL* equalled 2.73 μm).

The relative velocity (v) of the sarcomeres in interval i was determined from *SL* in the previous and following interval:

$$v_i = \frac{1}{2.73} \cdot \frac{SL_{i-1} - SL_{i+1}}{2 \cdot t} \quad (5)$$

where t is the duration of an interval. The *FV* is calculated separately for shortening and lengthening contractions. In the first case the equation (Hill 1938) was used:

$$FV_i = \frac{v_{max} - v_i}{v_{max} + \frac{P_0 \cdot v_i}{a}} \quad (v_i > 0) \quad (6)$$

In the rabbit digastric $\frac{a}{P_0} = 0.18$ and $v_{max} = 8.83\ s^{-1}$ at a temperature of 30°-35° C (Anapol et al. 1987). After correction for body temperature we used $v_{max} = 12.5\ s^{-1}$. For negative contraction velocities the increase in *FV* was approached by

$$FV_i = 1.5 - 0.5 \cdot \frac{v_{max} + v_i}{v_{max} - \frac{2P_0 \cdot v_i}{a}} \quad (v_i < 0) \quad (7)$$

This curve fitted experimental data (Van Ingen Schenau et al. 1988).

The *FP* was estimated, using previous data (Weijs et al. 1989a) as

$$FP_i = 0.0014 \cdot \exp\left(6 \cdot \frac{SL_i - 2.73}{2.73}\right) \quad (8)$$

The activation factor *FQ* depended on the time course of the EMG. The EMGs were registered by bipolar internal wire electrodes and digitized. Mean *iEMG* value per interval ($iEMG_i$) was determined. The duration of the interval (13 ms) was short enough to prevent any influence of the averaging process upon the outcome of the model calculations. The values were scaled using the maximal *iEMG* value recorded for that electrode (in mastication). Techniques and results have been described previously (Weijs et al. 1989b).

The *FQ* followed the *iEMG* with a delay caused by (1) the dynamics of the process of building up intracellular Ca^{2+} in reponse to depolarization and (2) the internal shortening process of the contractile element and extension of the series elastic element. Four muscle models were used to estimate this relationship.

1. For reference, a direct relationship (without time delay) was used between *iEMG* and *FQ*: (model E)

$$FQ_i = iEMG_i \quad (9)$$

2. In the second model the isometric twitch at optimal length of the masseter muscle was used as input data. The twitches were recorded in an experiment, described below and digitised at 1000 Hz. The response lasted about 70 ms and was represented by an average level of normalised force in six masticatory intervals following the stimulus (the vector *S*). It was assumed that in each interval a number of muscle fibres was recruited, proportional to the *iEMG* level, producing a twitch response whose amplitude was also proportional to that level. The factor FQ_i in any interval was now obtained by adding the contributions of twitch forces produced by the *iEMG* of that interval and of the preceding intervals: (model S, single twitch)

$$FQ_i = \sum_{j=1}^{i} iEMG_j \cdot S_{i-j+1} \quad (10)$$

where *S* is the normalised twitch force vector; a maximal force $FQ = 1$ was reached if a maximal *iEMG* level ($iEMG = 1$) was attained during at least six intervals.

3. The S-model ignores the fact that muscle fibres fire in partially or completely fused tetani. To account for partial fusion, the double twitch (D) model was developed. Here a double twitch, evoked by two stimuli at a 10 ms interval was used as input data. This response lasted longer (100 ms). The further procedure of model D was identical to the one followed for model S.

4. A previously published model (Otten 1987), assuming tetanic stimulation of muscle and a non-linear relationship between *iEMG* and *FQ* was also tested. Briefly, model O first derives the intracellular Ca^{2+} concentration ($[Ca^{2+}]$) produced by the *iEMG* by an empirically chosen differential equation

$$\frac{d[Ca^{2+}]}{dt} = C_r[Ca^{2+}]_{max} \cdot iEMG - C_r[Ca^{2+}] \quad (11)$$

The active state (Q) is calculated using an observed sigmoid relationship with $[Ca^{2+}]$ for an isolated muscle fibre

$$Q = \frac{[Ca^{2+}]^{2.6}}{[Ca^{2+}]_{0.5}^{2.6} + [Ca^{2+}]^{2.6}} \quad (12)$$

Finally *FQ* is calculated by a first order differential equation

$$\frac{dFQ}{dt} = C_q \left\{1 + \frac{FQ - Q}{2}\right\} \{Q - FQ\} \quad (13)$$

In (1), (2) and (3) C_r, C_q, $[Ca^{2+}]_{max}$ and $[Ca^{2+}]_{0.5}$ are constants. In our programme the equations were solved using 0.2 ms time intervals.

Isometric muscle force. Responses to a single or double stimulus were recorded from the anterior portion of the superficial masseter muscle. This area has a fibre type composition which is representative for the rabbit jaw muscles. Four adult rabbits were anaesthetised by intravenous administration of pentobarbital sodium. The jaw was closed and the head plus jaw were fixed in a metal frame by means of adjustable clamps. A skin incision gave access to the anterior masseter muscle. A 1-2 mm strip of the covering aponeurosis was detached from the zygomatic arch and attached to a force transducer. The temperature of the animal was maintained at 38° C by a heating pad while the muscle was kept at the same temperature, using a heat lamp and a thermistor. Supramaximal stimuli of constant duration (500 μs) and current (1-5 mA) were delivered by two intramuscular stainless steel electrodes (length 1 cm, diameter 1 mm). The transducer was mounted on a stage that could be rotated to adjust for the direction of pull of the fibres and translated to adjust fibre length to optimal length, i.e. the length where a tetanus of maximal amplitude was recorded. The preparations were also used to obtain simultaneous measurements of intramuscular EMG and force during spontaneous, voluntary isometric contractions. These occurred after applying mechanical stimuli to the oral mucosa. For a number of contractions *iEMG* values for each 13 ms interval were determined. The predictions of force for the different models were compared with the recorded force.

Forces during chewing. In nine rabbits and 41 masticatory sequences, each consisting of 10-30 chewing cycles, mandibular alveolar bone strain was recorded along with the EMGs of masticatory muscles. A rozette strain gauge, capable of measurement of magnitude and direction of the principal strains, was applied to the lateral side of the alveolar bone, just below the left cheek teeth, as previously described (Weijs and de Jongh 1977). According to this paper and Hylander et al. (1987) the bone strain is proportional to the bite force if the animal chews at the gauge (left) side. If it chews at the other side, the strain is proportional to the jaw closing moment of the muscles at the gauge side.

The EMG recordings of 4-6 electrodes were used to represent the muscles of the model. We used bipolar wire electrodes consisting of 0.05 mm diameter resin insulated copper wires with hooked bared ends (length of bare tip: 1 mm, distance between tips 1-2 mm). The signals were amplified 200-5,000× by differential amplifiers (bandwidth 30-10,000 Hz) and stored on analog tape. To account for the jaw closing muscles, for which no registration was available, a rough subdivision was made of the masseter muscle into a superficial, middle anterior deep and posterior deep

masseter, while the temporalis and medial pterygoid muscles were considered as single blocks, uniformly active. This can be justified because the average EMG patterns of the portions, belonging to such a larger section (e.g. temporalis, medial pterygoid, anterior deep masseter muscles) were virtually identical and the cycle to cycle amplitude variations were highly correlated. Recordings within one of the portions, belonging to these larger subdivisions, were treated as representative for the entire division. Although 4–6 electrodes represented no more than 50% of the above described muscle sections, recordings were normally made from the larger muscle sections (superficial masseter and medial pterygoids). A cinefilm, simultaneously recorded at 50 frames·s^{-1}, was used to determine the instants of maximal jaw opening, so that chewing cycles could be defined and the averaged length changes in the muscles could be synchronised with the EMGs.

The changes of calculated bite force (for left sided chewing) or muscle moment (for right sided chewing) in time were compared to the changes in bone strain. Furthermore, peak values of bite force or muscle moment per cycle were compared with peak strain. For each chewing sequence the correlation between these values was calculated to compare the performance of the different models. The correlation coefficients r were normalised to z scores (Dixon and Massey 1969): $z = 0.5 \ln\{(1+r)/(1-r)\}$. Differences between groups of z scores were evaluated by Student t-tests.

Results

Isometric contractions

Mechanical stimulation of the oral mucosa could, at moderate levels of anaesthesia, elicit low intensity, long lasting (0.3–2 s) bursts of spontaneous activity in the masseter muscle. Direct electrical stimulation of the same muscle strip elicited tetani with a 10–40 times higher force. Figure 2 shows two bursts of different duration. The iEMG and force of the muscle strip are shown together with the predictions of the S, D and O muscle models. In this case the iEMG was identical to the E model output because a single isometrically contracting muscle at resting length was involved.

A consistent finding was that the three models predicted quite accurately the rise and decay of the isometric force. If the rate of force increase or decrease was high, all three models were accurate within 15 ms. During natural mastication the activity bursts were shorter (0.1–0.2 s) and rates of change in force even higher than in the short spontaneous bursts such as the one of Fig. 2B. At steady-force levels or slow rates of change the models, in the order O, D and S, showed an increasing level of fluctuation in the predicted force (Fig. 2A) clearly following the fluctuations in mean iEMG. The wire electrodes picked up an interference EMG during normal masticatory activity. However, as the contraction level in these experiments was very low, a pattern of individual motor unit action potentials was registered. The resulting fluctuating mean iEMG did not correspond fully with the registered external force.

Although model O did 'better' in filtering away the EMG fluctuations, it showed an undesirable characteristic in not predicting any force below a certain low EMG level. This threshold effect was the result of the assumed sigmoid relationship between the intracellular [Ca^{2+}] and active state. Clearly, this assumption made

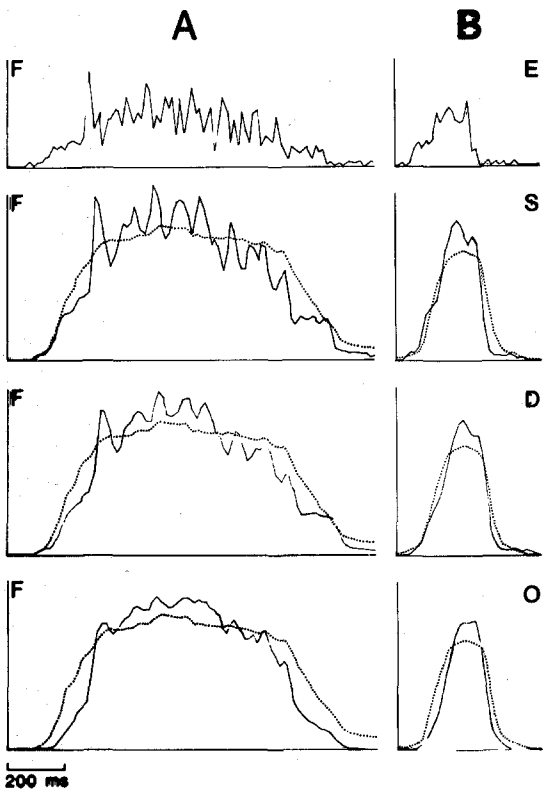

Fig. 2. Model predicted (*solid line*) and measured (*dotted line*) isometric force (F) of a strip of masseter muscle in a long lasting (**A**) and a brief (**B**) voluntary contraction. From top to bottom the integrated EMG (E) and the predictions of models S, D and O are shown

model O predict the initial rise of force too late and the final disappearance too early (Fig. 2A).

Mastication

The EMG and strain patterns for chewing three different foods differed slightly. The strain at the working (chewing) side was 2–3 times higher and somewhat different in principal strain direction from the strain at the non-chewing (balancing) side (Weijs and de Jongh 1977). Nevertheless, the fit of measured and predicted data depended neither on the side of the jaw where the strain was recorded, nor on the food masticated.

Figure 3 shows that a direct force prediction from the iEMG leads to a too early appearance and disappearance of the force. The predicted force reproduced the iEMG fluctuations, but did not match the strain gauge signal. The other models had filtering properties and this resulted in removal of the fluctuations and delay of the force relative to the iEMGs. In the great majority of the investigated cycles model S, nested in the jaw model, predicted best the time course of the strain. If model O was used the timing of the rise of strain and strain peak was predicted equally well, but the decay of strain occurred too late, although usually not as late as in the example shown. Use of the D model resulted in filtering properties that were too strong: both the strain peak and the strain decay occurred 15–25 ms later in

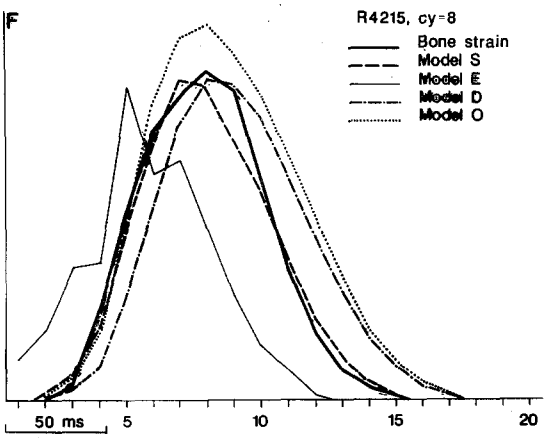

Fig. 3. Predictions by the four models of the bite force (*F*) against time in a single masticatory cycle together with recorded bone strain. The cycle has been subdivided in *20* intervals (*X-axis*) and starts and ends with maximum jaw opening

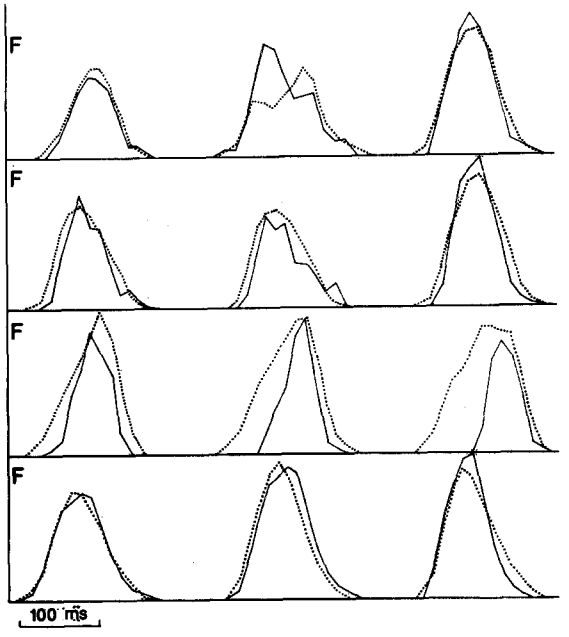

Fig. 4. Model S predicted bite force (*dotted line*) and measured bone strain (*solid line*) in 12 chewing cycles chosen from four (*top to bottom*) masticatory sequences recorded from different animals

the predictions than in reality. As the use of model S led to the best prediction of strain more examples of both good and bad fit for this model from four randomly chosen sequences are given in Fig. 4. The overall similarity between predictions and measurements was large and variations in the shape of the strain curve were generally well followed by the model. It appears, however, that the prediction for the rise of strain was sometimes poor. In cases where the strain pattern was irregular, the prediction of the shape of the strain curve was often poor, too.

Figure 4 shows that there was some correlation between the peak amplitudes of the measured and predicted signals within the sequences. A correlation be-

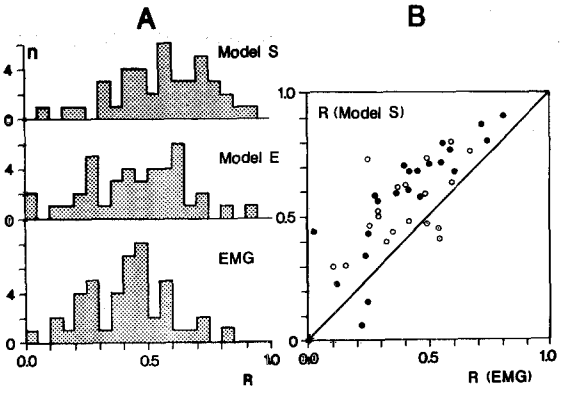

Fig. 5. A Frequency distribution of correlation coefficient *r* found between peak of bone strain per cycle and peak of EMG (*bottom row*), peak of model E predicted bite force (*middle row*) and peak of model S predicted bite force (*top row*), in 41 sequences. **B** Relationship between the model S/bone strain and EMG/bone strain correlation coefficients. In all but five sequences model S predicts bone strain better than the original EMGs. *Filled symbols*, chewing at gauge side. *Open symbols*, chewing at non-gauge side

tween EMGs of chewing muscles and strain amplitude was already present in the raw data: in cycles where strong EMGs were produced the bite force was high. The success of the proposed models could be assessed by determining if, and to what extent, the correlation between predicted peak force and measured peak strain was higher than the correlations in the raw data. Figure 5A shows a frequency distribution of the correlation coefficients (*r*) found in 41 sequences between the bone strain and (1) the iEMG itself (the mean value for the different available EMG channels of jaw closing muscles was taken), (2) the predictions of model E and (3) of model S. In this order, the mean *r* increased from 0.41 to 0.46 to 0.57. After normalisation of *r* a Student *t*-test showed that both the increase in correlation between the raw iEMG and model E ($t=2.0$, $P<0.05$) and the increase from model E to model S ($t=14.1$, $P<0.001$) were statistically significant. The percentage of the variance in peak strain amplitude (r^2) explained by model S was almost twice as high (32%) as the percentage explained by the iEMG signal (17%).

The improvement in the correlation coefficient could be demonstrated in 90% of the chewing sequences (Fig. 5B). In each sequence, using muscle model S, O or D in the jaw model made only a slight difference. No significant differences were found in the separate performance of the models on sequences of mastication of different foods nor on the separate performance on sequences where the strain gauge was on the working or the balancing side of the jaw. Figure 5B further shows that the level of the correlation coefficient between strain and model predicted force depended strongly on the initial level of the correlation between strain and EMG.

Discussion

The chosen model of a contractile element in line with an inextensible tendon is crude. It is known that muscle

fibres usually attach to tendons at an angle and that tendons can be stretched up to 3%–5% of their resting length (Van Ingen Schenau et al. 1988). For the pinnate rabbit digastric muscle 1 mm of whole muscle shortening has been shown to correspond to 0.7 mm of fibre shortening (Muhl 1982). Our data confirmed this for the other jaw muscles: the actual length change of the sarcomeres equalled 67% of the model predicted length change. The scatter of data was due to measurement error (histological determination of SL, SL variability over the length of the fibre, error in the determination of mandibular position) but also could have been caused by variation in pinnation angle between the different muscles.

We have adapted our SL estimates by a linear equation, producing the best fit to the observed data. Within the range of observed extensions, the relationship between SL and muscle length was linear and this indicates that tendon extensibility was probably unimportant. Furthermore it should be realised that FL and FQ were always, and FV usually, below unity so that the muscle force, even at maximal EMG, was rarely higher than 50% of the maximal force. Tendon extension thus remained limited to a few percent. It should be noted that the effect of tendon extensibility upon the speed of shortening of the fibres has been accounted for in models S, D and O.

The filtering response of model S and O ensured a realistic prediction of the rise and decay times of muscle force during isometric contraction. However, during the contraction fluctuations in force were predicted that did not correspond to the smooth force signals. Our bipolar wire electrodes with 1 mm bare ends normally picked up an interference EMG from a small area of muscle. In the isometric experiments it was expected that the area of muscle contributing to the force was larger than the EMG pick-up area. Moreover, the observed spontaneous isometric contractions had a very low strength and the EMG recorded showed individual motor unit action potentials. We suspect that this EMG was no longer representative and that for that reason the fluctuations in the processed EMG had little relationship with the force signal.

Not enough data were collected to establish a relationship between iEMG and isometric force. Most investigations use a linear relationship and this is supported by the majority of experimental data (Basmajian and de Luca 1985). Otten (1987) assumed that a non-linear relationship existed between intracellular $[Ca^{2+}]$ and isometric force. However, active muscle contains fibres with different $[Ca^{2+}]$. As the relationship was non-linear, calculating muscle isometric force from average $[Ca^{2+}]$ was not correct.

The validation experiments had three important shortcomings: (1) not all the muscles that contribute to the alveolar bone strain were recorded, (2) instead of the actual movement per cycle the average movement of the jaw was used as input data, and (3) the different muscles in the system may contribute differentially to the bone strain, even if they exert the same force.

The fact that nevertheless a surprisingly good correspondence exists between observed and predicted forces can probably be explained by two factors, (1) stereotyped movements, such as demonstrated by the 3-D movement patterns of the jaw (Schwartz et al. 1989) and (2) relatively fixed relationships between the peak amplitudes of the different contracting muscles. The constant proportions of activity levels of different muscles could be deduced from relatively high mutual correlations between the EMGs of the muscles and from the fact that the direction of the principal strains of the alveolar bone varied but little from cycle to cycle (Weijs and de Jongh 1977). Sometimes the predicted force increased prior to the measured strain (Fig. 4c). We suspect that the elastic properties of the food mass between the occluding teeth delayed the effect that the muscular forces had on the deformation of the bone, measured as strain. In the jaw model a rigid contact was assumed between the teeth at all degrees of jaw closure.

In dynamic contractions the FL, FV and twitch contraction characteristics became important. In natural chewing the FL factor varied from 0.7 (at a SL of 2.3 μm) to 1.0 (SL = 2.7 μm). The FV factor exerted a much stronger influence upon the muscle force as it varied between 0.25 (4 fibre lengths $\cdot s^{-1}$) to 1.4 (minus 2 fibre lengths $\cdot s^{-1}$, i.e. extension). We have concluded that the force-velocity property was the most dominant influence on the mechanics of the chewing system next to the level of muscle activation (Weijs and van Ruijven 1990).

The chosen FV constants (v_{max} and a/P_0), the shape of the twitch and the constants C_r and C_q in the Otten model apply to whole muscle. Hence the models produced correct results as long as the group of active motor units was representative of the whole muscle with respect to fibre type composition. The FV parameters and twitch shape differed considerably for slow and fast units and it was shown experimentally (Phillips and Petrofsky 1983) that the properties of the whole muscle depend on the relative participation of the slow and fast motor units in a contraction. For limb muscles recruitment of slow units at low force levels, followed by additional recruitment of fast units has been demontrated (Armstrong and Laughlin 1985). Therefore, at low contraction levels, model results with parameters for whole muscle may be erroneous. Unfortunately, the EMG gave no unambiguous clues as to the participation of motor unit types. It has been demonstrated that in mastication of hard foods the level of muscle contraction is extremely high, close to maximal activation (Hagberg 1986). In that situation, most or all units are recruited and the model results will not be biased.

This study has shown that the EMG response of the masticatory muscles, known to fire with different amplitudes and partially asynchronously (Weijs et al. 1989b), contains sufficient information to predict the rise and fall of the load on the alveolar bone at the chewing side and at the non-chewing side. Furthermore, from the stochastic variation in the EMG signals from one chewing cycle to another the variation in peak load and in shape of the load curve could be predicted.

The accuracy of the prediction was limited. However, the validation experiments themselves were subject to measurement error.

The original EMG signals were all mutually correlated and correlated to the strain. Use of model E accounted for the difference in timing of contraction of the different muscles, for their differences in maximal strength and orientation and for their FL and FV relationships. Such a model increased significantly the amount of the explained variance in strain values, relative to the average amount explained by the individual EMG signals. Use of the models that took into account the time dependence between EMG and muscle force improved the prediction of peak amplitude.

The three models did not differ greatly in the amount of improvement they made. This was surprising as model S assumes that all motor units fire unfused twitches, while model O assumes fused tetani and model D is intermediate. This implies that the firing rates of the individual motor units do not matter greatly in determining the relationship between EMG and muscle force in time. It further implies that nothwithstanding the basic shortcoming of the EMG signal of lacking information about the contraction state of single units, it can be used to estimate mechanical output. Of the three models, model S seemed to give a slightly better prediction of muscle force than the other two. Apart from the shape of the twitch and FV characteristics, available in the literature, it needed neither special physiological parameters, nor fitting procedures for parameters.

Our model can be applied to estimate in vivo contractile forces of muscles participating in complex movement activities like walking and chewing, both in healthy subjects and patients. Identical external loads can be produced by different cocontraction patterns of the same set of muscles. However, as these muscles have different areas of attachments, they may generate different internal stresses in bones and loading patterns of joints. Knowing the mechanical contributions of the separate agonists is essential to quantify the internal loads and stresses and assess risk factors for the fracture of bones or overloading joints. We will use the model to provide estimates of temporomandibular joint loading during normal and abnormal use of the jaw muscles.

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References

Anapol FC, Muhl ZF, Fuller JH (1987) The force-velocity relation of the rabbit digastric muscle. Arch Oral Biol 32:93–99

Armstrong RB, Laughlin MH (1985) Metabolic indicators of fibre recruitment in mammalian muscles during locomotion. J Exp Biol 115:201–213

Basmajian JV, de Luca CJ (1985) Muscle alive. Their functions revealed by electromyography. Williams and Wilkins, Baltimore

Dixon WJ, Massey FJ (1969) Introduction to statistical analysis. McGraw-Hill, New York

Dowling JJ, Norman RW (1988) The prediction of individual muscle forces at the human elbow. In: De Groot G, Hollander AP, Huijing PA, van Ingen Schenau GJ (eds) Biomechanics XI-A. Free University Press, Amsterdam

Hagberg C (1986) The amplitude distribution of electromyographic activity of mastication muscles during unilateral chewing. J Oral Rehabil 13:567–574

Hill AV (1938) The heat of shortening and the dynamic constants of muscle. Proc R Soc Lond [Biol] B 76:136–195

Hof AL, van den Berg JW (1981) EMG to force processing III: estimation of model parameters for the human triceps surae and assessment of the accuracy by means of a torque plate. J Biomech 14:771–785

Hylander WL, Johnson KR, Crompton AW (1987) Loading patterns and jaw movements during mastication in Macaca fascicularis: a bone strain, electromyographic, and cineradiographic analysis. Am J Phys Anthropol 72:287–314

van Ingen Schenau GJ, Bobbert MF, Ettema GJ, de Graaf JB, Huijing PA (1988) A simulation of rat EDL force output based on intrinsic muscle properties. J Biomech 21:815–824

Inman VT, Ralston JB, Sanders CM, Feinstein B, Wright EW (1952) Relation of human electromyogram to muscular tension. Electroencephalogr Clin Neurophysiol 4:187–194

Lippold OCJ (1952) The relation between integrated action potentials in a human muscle and its isometric tension. J Physiol 117:492–499

Muhl ZF (1982) Active length tension relation and the effect of muscle pinnation on fiber lengthening. J Morphol 173:285–292

Muhl ZF, Grimm AF, Glick PL (1978) Physiological and histological measurements of rabbit digastric muscle. Arch Oral Biol 23:1051–1059

Olney SJ, Winter DA (1985) Predictions of knee and ankle moments of force in walking from EMG and kinematic data. J Biomech 18:9–20

Otten E (1987) A myocybernetic model of the jaw system of the rat. J Neurosci Methods 21:287–302

Phillips CA, Petrofski JS (1983) Velocity of contraction of skeletal muscle as a function of activation and fiber composition: a mathematical model. J Biomech 13:549–558

Ralston HJ (1961) Uses and limitations of electromyography in the quantitative study of muscle function. Am J Orthod 47:521–530

Schwarz G, Enomoto S, Valiquette C, Lund P (1989) Mastication in the rabbit: a description of movement and muscle activity. J Neurophysiol 62:273–287

Weijs WA, de Jongh HJ (1977) Strain in mandibular alveolar bone during mastication in the rabbit. Arch Oral Biol 22:667–675

Weijs WA, van der Wielen-Drent TK (1982) The relationship between sarcomere length and activation pattern in the rabbit masseter muscle. Arch Oral Biol 28:307–315

Weijs WA, van der Wielen-Drent TK (1983) Sarcomere length and EMG-activity in some jaw muscles of the rabbit. Acta Anat 113:178–188

Weijs WA, van Ruijven LJ (1990) Models of masticatory mechanics: their reliability, resolving power and usefulness in functional morphology. Neth J Zool 40:136–152

Weijs WA, Brugman P, Klok EM (1987) The growth of the skull and jaw muscles and its functional consequences in the New Zealand rabbit (Oryctolagus cuniculus L.). J Morphol 194:143–161

Weijs WA, Korfage JAM, Langenbach GJ (1989a) The functional significance of the position of the center of rotation for jaw opening and closing in the rabbit. J Anat 162:133–148

Weijs WA, Brugman P, Grimbergen CA (1989b) Jaw movements and muscle activity during mastication in growing rabbits. Anat Rec 224:407–416

Winters JM, Stark L (1987) Muscle models: what is gained and what is lost by varying model complexity. Biol Cybern 55:403–420