Clin Oral Invest (2011) 15:737–747
DOI 10.1007/s00784-010-0436-4

ORIGINAL ARTICLE

Muscle and joint forces under variable equilibrium states of the mandible

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Received: 25 September 2009 / Accepted: 11 June 2010 / Published online: 29 June 2010

Abstract It is well established that subjects without molars have reduced ability to comminute foods. However, epidemiological studies have indicated that the masticatory system is able to functionally adapt to the absence of posterior teeth. This supports the shortened dental arch concept which, as a prosthetic option, recommends no replacement of missing molars. Biomechanical modeling, however, indicates that using more anterior teeth will result in a larger temporomandibular joint load per unit of bite force. In contrast, changing bite from incisor to molar position increases the maximum possible bite force and reduces joint loads. There have been few attempts, however, to determine realistic joint loads and corresponding muscular effort during generation of occlusal forces similar to those used during chewing with intact or shortened dental arches. Therefore, joint and cumulative muscle loads generated by vertical bite forces of submaximum magnitude moving from canine to molar region, were calculated. Calculations were based on intraoral measurement of the feedback-controlled resultant bite force, simultaneous electromyograms, individual geometrical data of the skull, lines of action, and physiological cross-sectional areas of all jaw muscles. Compared to premolar and canine biting, bilateral and unilateral molar bites reduced cumulative muscle and joint loads in a range from 14% to 33% and 25% to 53%, respectively. During unilateral molar bites, the ipsilateral joints and contralateral muscles were about 20% less loaded than the opposing ones. In conclusion, unilateral or bilateral molar biting at chewing-like force ranges caused the least muscle and joint loading.

Keywords Shortened dental arch · Joint forces · Muscle forces · EMG · Bite forces

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Introduction

Clear relations exist between dental state and biomechanical masticatory function. It is well established that subjects without molars have a reduced ability to comminute test foods [1–3]. However, epidemiological studies suggest that they still retain sufficient chewing ability to maintain reasonable health [4]. Furthermore, there is no clinical evidence that a shortened dental arch (SDA) increases the likelihood of temporomandibular joint disorders [5]. Nonetheless, biomechanical modeling indicates that using more anterior teeth will result in a larger load per unit of bite force within the temporomadibular joints (TMJ). In contrast, changing the location of the bite point from the incisor to the molar region increases the maximum possible bite force, while reducing joint loads, as model calculations have shown [6–10]. Experiments with maximum muscle activation confirmed the increase of bite force under anteroposterior change of the bite point and documented as mandatory consequence that bite force moments (i.e., the products of bite forces and lever arms relative to the intercondylar axis) calculated for different bite locations were largely kept constant under these conditions [11]. On the other hand, decreasing muscle activity was shown with bite points moving anteroposteriorly when the bite force was kept constant [12].

In a study using pressure-sensitive foils, it was found that cumulative muscle activity, maximum bite force, and joint forces decreased under maximum bite when the antagonistic tooth contacts were sequentially reduced from the molar to the incisor region [13]. These experimental results may suggest that muscle recruitment under in vivo conditions is more complex than pure model calculations are able to simulate. Mechanical advantage, i.e., the ratio of the moment arm of the muscle force to the moment arm of the bite force [6, 7], neuromuscular control, and variable vertical jaw gap during biting [14], only to list a few essential parameters, determine the recruitment strategy which motor systems utilize for specific tasks. Therefore, predictions, e.g., inferred from bite experiments under variable SDAs with maximum effort, should not be transferred unscreened to conditions with submaximum bite forces similar to those used during chewing. Hence, the conclusion that moving any constant bite force from canines to molars would decrease cumulative muscle and joint forces may be qualitatively true, but it must be validated for submaximum biting conditions to yield realistic quantitative data. Such data are also of importance for basic research dealing, for example, with load capacitance of joint tissues, or clinical questions regarding correlations between load distribution and physiological cross-section of the various masticatory muscles.

TMJ and muscle forces are not accessible to direct measurements in humans, but have to be computed. Therefore, in previous decades, numerous investigations were carried out to estimate TMJ and muscle forces on the basis of biomechanical modeling. Theoretical descriptions of the statics of the jaw system have been accomplished using two-dimensional [6, 7, 15–17] or three-dimensional models implementing optimization algorithms [18–20]. Since such theoretical calculations imply several assumptions, they need to be validated by data measured in vivo to yield realistic quantitative results. Electromyographic recordings (EMGs) of specific muscles, bite forces, and anatomical data were used to validate model predictions [13, 18, 21–23].

The objective of this investigation was to load the masticatory system with vertical bite forces (50-200 N) in the range of chewing forces [24–26] simulating unilateral molar, bilateral molar, bilateral premolar, and bilateral canine bites. Muscle and joint forces should be calculated on the basis of 3-D models using force-controlled electromyograms of all jaw muscles, subject-related geometrical data of the skull, and individually calculated intrinsic muscle strength (P) all gathered from one specific sample. By intending to establish realistic quantitative data for muscle effort and joint forces, we aimed at validating the theoretical prediction that under constant chewing-like bite forces, cumulative muscle effort and joint load will substantially be reduced when the bites move from the canine to the molar region.

Material and methods

Subjects

Ten healthy male subjects (age range: 23-41 years) gave written informed consent to participate in this study. The subjects had Angle class I or mild class II dentition. Exclusion criteria were skeletal anomalies (e.g., short faced or long faced) or distinct malocclusions. The study was approved by the Ethics Committee of the University Medical Center Freiburg, Germany (No. 25/02, amendment 04).

In vivo measurements

Intraoral force measurement

Intraoral force measurement was accomplished as recently described [27]. Three force transducers (Fig. 1) equipped with strain gages (6/120 LY 11; Hottinger Baldwin Messtechnik, Darmstadt, Germany) and connected to a

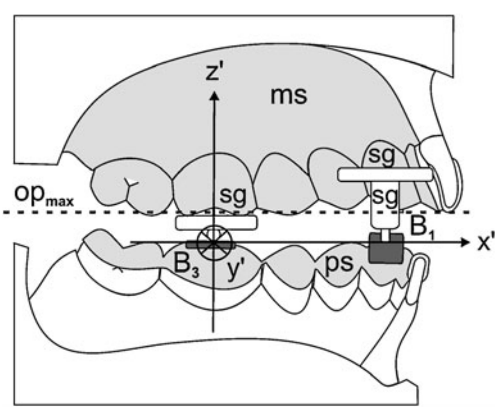

Fig. 1 Scheme of intraoral force measuring device used in the experiments; B_1, B_2, B_3 force transmission points; x', y', z' coordinate system in the occlusal plane of the maxilla; op_{max} oclusal plane of the maxilla, *sg* strain gage, *ps* plastic splint, *ms* metal splint

metal splint were placed parallel to the maxillary occlusal plane bilaterally over the first molars and midsagittally between the canines. The posterior transducers measured purely vertical forces, while the midsagittal transducer transmitted vertical and horizontal forces [23]. The mandibular teeth were covered by a plane plastic splint with metal plates in the region of force transmission. A perforation in the anterior plate enabled a joint connection between a maxillary bearing pin and the mandibular splint. The devices were prepared in centric relation, which was accomplished by rotational opening of the jaws. Both splints which were inserted using temporary cement, caused, on average, a jaw separation of 4.5 mm between the first molars. The configuration simulated equilibrium comparable to natural intercuspation by reducing the bite force transmission across multiple contact points of the dental arches by one anterior and two posterior transmission points. The signals were amplified (DMD 20 A; Hottinger Baldwin Messtechnik) and digitized (sampling rate: 1000 Hz).

Feedback

During the experiments, the intraorally measured force components were shown to the subjects on a screen as a resultant force vector [28]. The target values were marked on the display. The angle ϕ (angle between the x'-axis and the projection of the force vector onto the x'-, y'- plane, cf. Fig. 2) and the angle θ (angle between the z'-axis and the force vector) of the spatial force vector, which was generated by the subjects, were displayed in a planar coordinate system as a vector. Angle ϕ was plotted in circumferential and angle θ in radial direction. Therefore, a pure vertical force corresponded to $\theta=0°$, a pure horizontal force to $\theta=90°$. The amount of force was shown on the display as an additional vertical bar with scaling. When the test person reached the marked task values, measurements were started.

EMG

Bipolar surface electrodes measured bilaterally the EMG of the masseter, anterior temporalis, posterior temporalis, and anterior digastric muscle. The self-adhesive disposable electrodes (Ag/AgCl, recording diameter, 14 mm; center-to-center, 20 mm) were placed parallel to the longitudinal axis of the muscles. The space for the posterior temporalis electrodes was prepared by discrete shaving of the hairline around the ear. Before application, the skin was cleaned with 70% ethanol. An extraoral approach was used to gain access to the medial and inferior lateral pterygoids by bipolar wire electrodes, as previously described [29]. The common electrode was positioned in the neck above the seventh vertebra. The EMG signals were differentially amplified (EM 100 Biopac, Santa Barbara, CA, USA; frequency response 1-5,000 Hz), sampled at 1,000 Hz simultaneously with the force signals, and band-pass filtered (1-500 Hz).

Tasks

At first, the force transducer and the plastic splint were mounted on the tooth rows. Controlled by the displayed force signals, the vertical force components at the three transmission points were equally balanced under a constant resultant force of 100 N by occlusal foil-aided grinding (double folded 12 μm, GHM Hanel, Nürtingen, Germany) [28]. Prior to the experiments, the subjects generated vertical bite forces ranging from 50 to 400 N.

Thereafter, the measuring device was removed and the electrodes were attached in the manner described above. The subjects were instructed to bite three times at maximum effort in maximum intercuspation for about 3 s. To accomplish maximum activation of the lateral pterygoid muscle, protrusive, laterotrusive, and opening jaw movements against the resistance of the examiner's hand were performed. Maximum activation of the posterior temporalis was provoked by forceful voluntary retrusion of the mandible. The same task as well as opening against resistance was used to receive maximum EMG values for the anterior digastric. All activations were repeated three times. To produce maximum force, the subjects received repeated vocal encouragement.

Four equilibrium states (ESs) were simulated (Fig. 2); (1) bilateral canine biting, simulated by biting on the

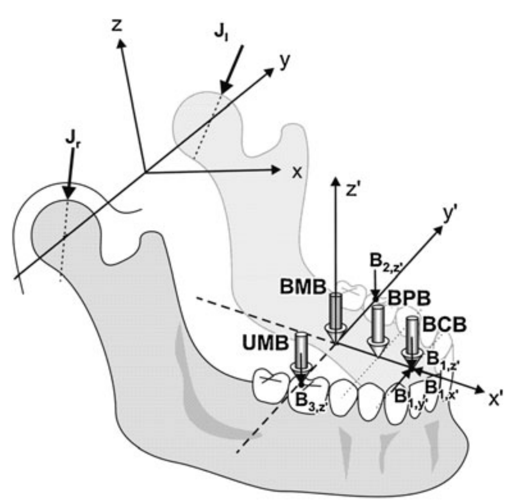

Fig. 2 Reference planes and their orientation to the location of force measurement; *x*, *y*, *z* coordinate system in the Frankfort horizontal plane; x', y', z' coordinate system in the occlusal plane of the maxilla; $B_{1,x'}$, $B_{1,y'}$, $B_{1,z'}$, $B_{2,z'}$, $B_{3,z'}$ transmitted force components; J_r, J_l right and left joint reaction forces (as resultant forces acting on the mandible), *BCB* bilateral canine biting, *BPB* bilateral premolar biting, *BMB* bilateral molar biting, *UMB* unilateral molar biting

midsagittaly placed anterior force transducer (BCB), (2) bilateral premolar biting, simulated by the resultant force vector of the identically balanced three vertical force components (BPB), (3) bilateral molar biting, simulated by bilateral biting on the posterior force transducers (BMB), and (4) unilateral molar biting, simulated by unilateral biting on one of the posterior transducers (UMB). To achieve all simulations in one single session, the anterior bite point was raised by a bisected metal sphere (diameter, 1.5 mm), which was placed in the anterior perforation to simulate BCB. To accomplish UMB and BMB, 1 or 2 posterior bite points on the lower splint were selectively raised by small steel plates (thickness, 0.5 mm), which disengaged completely the vertical contact of either the contralateral and anterior (UMB) or the anterior force transmission point (BMB). In both cases, the horizontal force transmission in the anterior perforation was maintained in order to guarantee purely vertical bite forces.

After reinsertion of the devices, the subjects generated exclusively vertical bite force vectors (BF) of 50, 100, 150, 200 N. Each BF was performed three times for about 3 s. The follow-up of the ES and the BF was selected at random order.

Analysis of EMG data

The point in time was determined at which the test person was closest to the given force vector, i.e., at which the error $e = \left|\vec{F}_{\text{measured}} - \vec{F}_{\text{target}}\right| / \left|\vec{F}_{\text{target}}\right|$ was minimal. The EMG value (rectified by root mean square algorithm) of a 400 ms interval around this point was employed and normalized with the maximum EMG activity, which was averaged out of a 400-ms interval around the peak activity of the respective muscle. These relative EMG values (U_{rel}; MVC[%]) of the muscles were used for the computations. Intraindividual scatters for the same tasks were clarified using coefficients of variation (cv).

Force calculations

Anatomical geometry

For each subject, a 3D-model of the musculature and structures relevant for the calculations was reconstructed, as previously described [18], using horizontal and frontal magnetic resonance tomograms taken in maximum intercuspation (slice distance: 4 mm). From the muscle models, the lines of action (lines through the centers of the muscle attachment areas [30]) were acquired. For the calculation of $A_i = V_i / l_{f,i}$ (V_i, reconstructed muscle volume; $l_{f,i}$, fiber length [31]), the tendinous tissue was subtracted from the muscle volume based on previous studies [31]. The model also served to identify the Frankfort horizontal plane (x-, y-plane), the occlusal plane (x'-, y'-plane), and the position of the force transmission points (B_1, B_2, B_3; Fig. 2). Using these data, all force vectors were transformed to the x-, y-, z-coordinate system, i.e., the Frankfort horizontal plane was taken as reference. Due to rotation of the mandible around the intercondylar axis because of the sensors, the lines of action of the muscles were corrected with respect to their insertion point, taking into account jaw openings of 4.5 mm in the molar region.

Computation of muscle, joint, and bite forces

Muscle, joint, and bite forces which had to fulfil the six equilibrium conditions were calculated as previously described [27, 28]. Using an appropriate force law, muscle forces were given by $\overrightarrow{F}_i = P\, A_i \cos\alpha_i \left\{c \cdot U_{rel,i} + (1-c) U^2_{rel,i}\right\} \overrightarrow{e}_i$, where the best parameter set of c and P was gained by a least squares fit using the data for biting tasks ranging from 50 to 400 N (α_i was based on previous studies [31]). However, to be able to achieve equilibrium for each task, the parameter P was computed each time via the equilibrium conditions. Since line of action, physiological cross-section, and relative electric activity were determined for each muscle, and c gained as described above, P was the only parameter needed to compute the 36 muscle force components. The joint forces, which were supposed to intersect the line connecting the centers of the condyles (y-axis), can only be transmitted by compression. Assuming negligible deformations of the mandible and condylar movements along the y-axis to be restricted in medial direction only, it may be concluded that the y-component of the reaction force has to vanish for one joint. This finally leads to a system of six equations for six unknowns. Since the joint force components disappear from the balance of momentum with respect to the joint axis, P (and consequently the muscle forces) can be determined directly from this equation. Relations for the five joint force components are given by the five remaining equilibrium conditions. More detailed information of the mathematical procedure is available in the Appendix.

Data analysis and statistics

Muscle and joint forces were normalized with the corresponding BF. Normalized electric muscle activities (MVC[%]), absolute and normalized forces were described by mean values and standard deviations (SDs). Muscle and joint load differences under the various ESs were also expressed as percentage of the forces developed under BMB. To obtain cumulative muscle loading for the various ESs, subjects' individual muscle forces

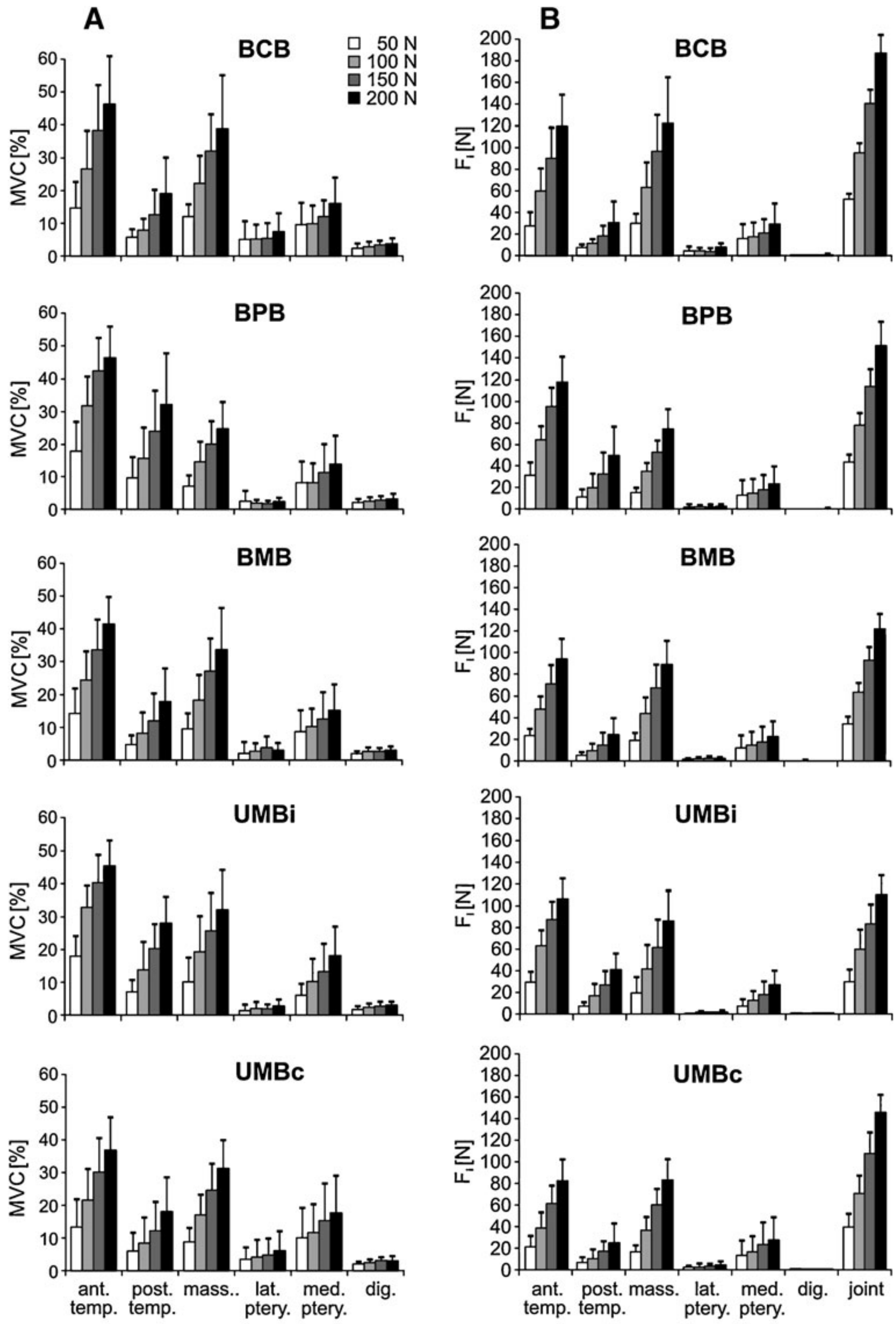

Fig. 3 Group mean and standard deviations of electric activity and the absolute muscle and joint forces illustrated for the subjects' right side (n=10). Data for identical tasks of the left and right side are pooled. **A** Electric muscle activity normalized with activity of maximum voluntary clenching (MVC [%]); **B** muscle and joint forces (F_i[N]). *Different shades of bar plots* (left to right) encode F_{res}=50, 100, 150, 200 N; *BCB* bilateral canine biting; *BPB* bilateral premolar biting; *BMB* bilateral molar biting; *UMBi* unilateral molar biting, ipsilateral side; *UMBc* unilateral molar biting, contralateral side; *ant. temp.* anterior temporalis; *post. temp.* posterior temporalis; *mass*. masseter; *lat. ptery.* lateral pterygoid; *med. ptery.* medial pterygoid; *dig.* digastric

were averaged over the BFs and added for each ES. The influence of BF and ES on joint and muscle forces was examined with a two-way analysis of variance with repeated measures (analysis of variance, ANOVA) for all possible paired ES combinations. Post hoc tests were accomplished by paired t tests. The value α=0.05 was assumed as significance level.

Results

Variability of measured data

The mean intraindividual variability (cv) of the EMG data for three measurement repetitions of maximum effort tasks amounted to 13.7±3.5%, for the task repetitions to

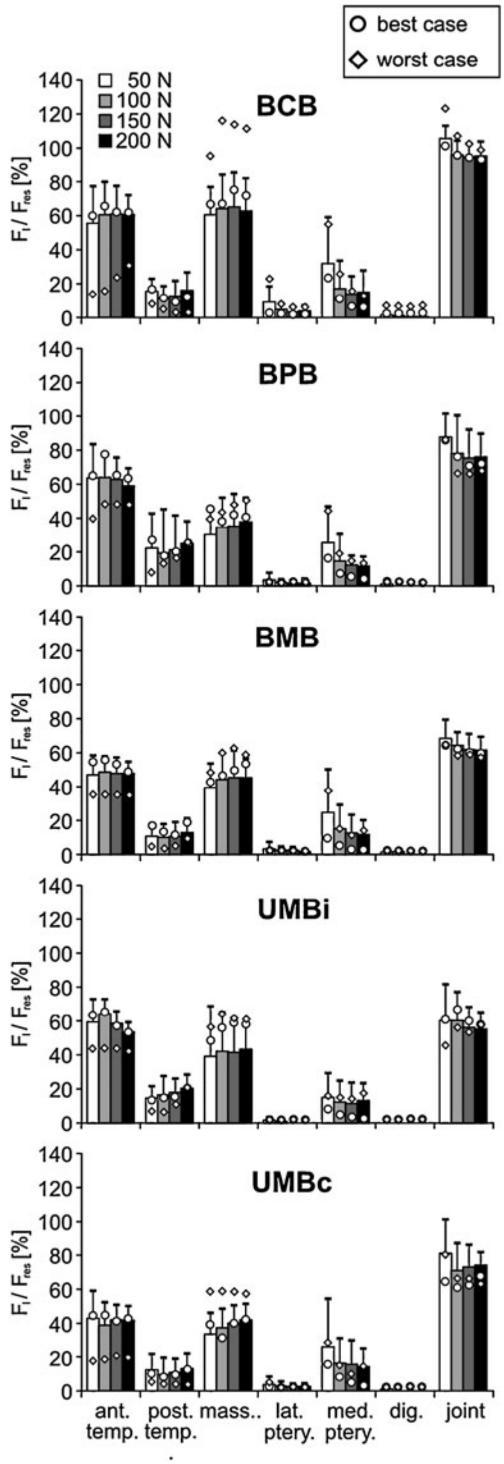

Fig. 4 Group mean and standard deviations of the normalized muscle and joint forces illustrated for the subjects' right side. Data for identical tasks of the left and right side are pooled. Best-fitting (*empty circle*) and worst-fitting (*empty diamond*) cases are also depicted (n=10). F_i/F_{res}= forces referred to the resultant force; *different shades of bar plots* (left to right) encode F_{res}=50, 100, 150, 200 N; *BCB* bilateral canine biting; *BPB* bilateral premolar biting, *BMB* bilateral molar biting; *UMBi* unilateral molar biting, ipsilateral side; *UMBc* unilateral molar biting, contralateral side; *ant. temp.* anterior temporalis; *post. temp.* posterior temporalis; *mass.* masseter; *lat. ptery.* lateral pterygoid; *med. ptery.* medial pterygoid; *dig.* digastric

10.4±3.1%. The mean deviation of the measured force vectors from the target force vectors was less than 5%.

Calculations based on the in vivo measurements

Average left and right side data for corresponding BFs were pooled (Fig. 3a, b), because bilateral normalized EMGs, absolute joint forces, and homonymous muscle forces showed no significant differences (p>0.05). Normalization of muscle and joint forces by bite forces (F_i/F_{res} [%]) showed similar ratios for all muscles and bite force levels (Fig. 4).

ANOVA of the normalized joint reaction forces revealed a significant (p<0.05) interaction between BF and ES for all paired ES comparisons, with the exception of BMB vs. ipsilateral UMB. Post hoc tests showed that the joint forces between BMB, BCB, and BPB differed significantly (p<0.05) for all pairwise comparisons at all BF levels (Figs. 3b, 4). For ipsilateral and contralateral UMB, joint forces differed significantly only between BF levels of 150 and 200 N. BMB and ipsilateral UMB led to least joint forces (Figs. 3b, 4). Averaged normalized ipsilateral and contralateral joint forces for UMB resembled those for BMB (Figs. 5a, 6b).

ANOVA for the individual muscle forces showed a significant (p<0.05) interaction between BFs and ESs for specific muscles. *Post hoc* tests revealed significant (p<0.05) differences of muscle forces for the anterior temporalis between BMB vs. BPB, BMB vs. BCB, and ipsilateral vs. contralateral UMB at all BF levels. The posterior temporalis displayed significant (p<0.05) differences between BPB vs. BMB and ipsilateral vs. contralateral UMB for all BFs. The masseter showed significant differences (p<0.05) between BCB vs. BMB and BPB for all BF levels. The medial pterygoid, lateral pterygoid, and digastric muscle exhibited no significant change of muscle forces between the various ESs at all BF levels (Figs. 3b, 4). The anterior temporalis was more active (p<0.05) under BPB and ipsilateral UMB. In contrast, BCB, BMB and contralateral UMB showed an approximately equal force ratio between masseter and anterior temporalis (Fig. 4). Analysis of the individual data revealed that even in the best fitting case, clear deviations from the average force distributions could be observed (Fig. 4).

Cumulative muscle forces for BMB were significantly (p<0.05) smaller than those for BCB, BPB, and ipsilateral UMB (5B). Averaged ipsilateral and contralateral muscle forces for UMB resembled those for BMB (Fig. 6a). Analysis of the data on a subject's basis showed that these patterns could also be observed in each individual case

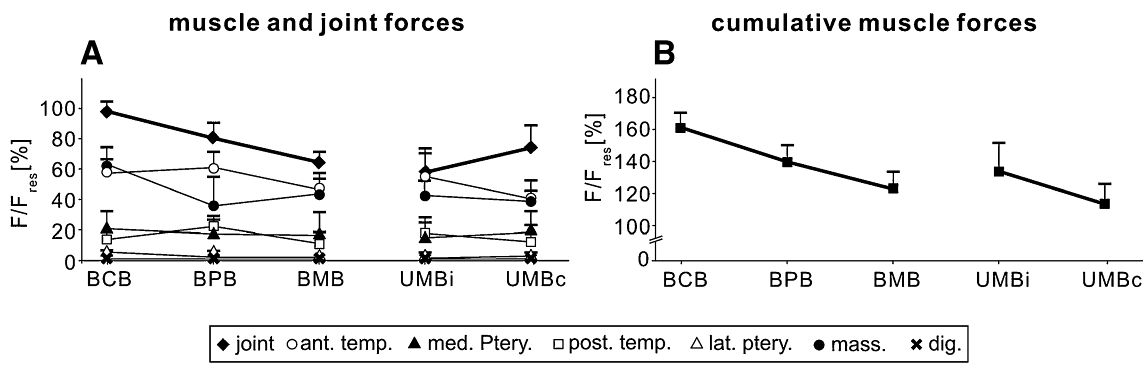

Fig. 5 Muscle and joint forces. **A** Calculated F_i/F_{res} for individual muscles and the jaw joint of one side, averaged over the four-bite force tasks (n=10). **B** Calculated cumulative muscle force=sum of F_i/F_{res} (mean of the four-bite force tasks) of all muscles for each equilibrium state (n=10)

(Fig. 6a). The average muscle and joint load variations as percentage of bite forces expressed as relative differences to BMB increased in the range of 14-33% and 25-53%, respectively (Table 1).

Discussion

During bilateral submaximum biting, muscle and TMJ forces increased significantly when the jaw gap was kept constant and identical resultant bite forces moved from the molar to the canine region. During unilateral molar biting, the ipsilateral TMJ is about 20% less loaded than the contralateral joint, whereas cumulative muscle forces are 20% larger on the ipsilateral side. These findings were consistently confirmed on an individual subject's basis. In conclusion, the hypothesis that cumulative muscle effort and joint load will substantially be reduced during constant submaximum bites, when the bite point moves from canine to molar region, can be confirmed. The results are largely in line with predictions based on previous model calculations [6–10, 20]. However, our findings extend them to submaximum bites. Furthermore, for the first time, quantitative results are presented for cumulative muscle and joint forces on the basis of comprehensive feedback-controlled in vivo measurements and individual 3-D model calculations from one sample.

Comparison of our calculations with those also based on validated 3-D models [13, 20, 32] are difficult, because only one study presented simultaneously measured quantitative data for joint, muscle, and bite forces for the investigated SDAs under bilateral biting [13]. Conversely, two other publications referred to unilateral biting and presented only data for premolar and molar or molar bites, respectively [20, 32]. Table 2 shows the collected data from the three study reports which partly had to be estimated from figures [13] or recalculated from figures presenting single muscle forces [20], and contrasts them with our

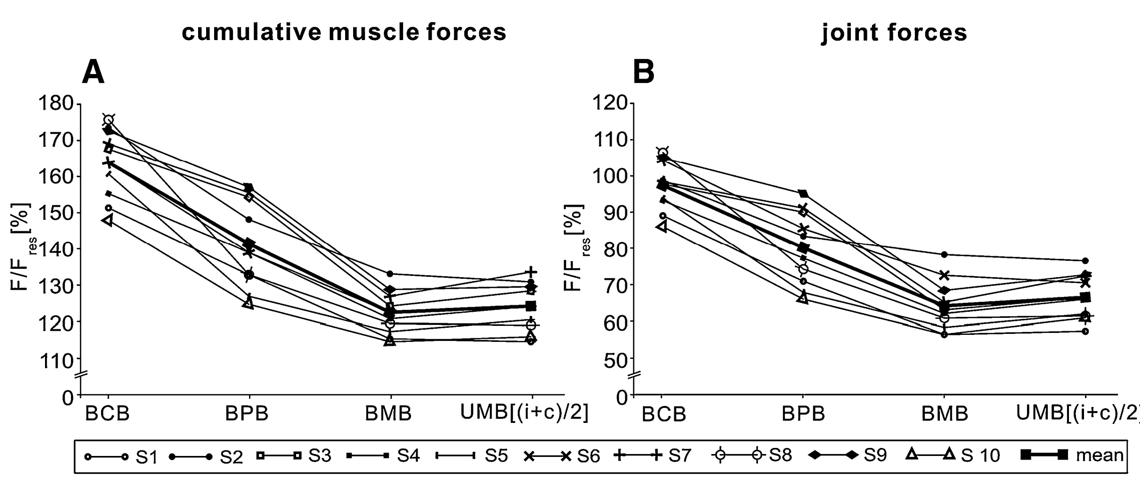

Fig. 6 Calculated cumulative muscle and joint forces as depicted in Fig. 5 on an individual subject's base (S1-S10) for each equilibrium state. Values for UMBi and UMBc are averaged. **A** Calculated F_i/F_{res} for individual muscles of one side, averaged over the four-bite force tasks. **B** Calculated joint forces F_i/F_{res} of one side, averaged over the four-bite force tasks

Table 1 Cumulative muscle and joint forces as percentage of bite forces

ES	BMB	BPB	BCB
Cumulative muscle and joint forces (BF%)			
Joint forces	64	80	98
Muscle forces	122	140	162
Relative differences (%) to BMB			
Joint forces	-	25	53
Muscle forces	-	14	33

Data are averaged over the four-bite force tasks (n=10) and all bite forces

Forces are normalized with the respective bite force and averaged over the four tasks (n=10)

ES equilibrium state, *BMB* bilateral molar bites, *BPB* bilateral premolar bites, *BCB* bilateral canine bites

results. It needs to be mentioned that the data computed from pressure sensitive foils [13] had to be corrected with regard to the location of the resultant bite force, i.e., results for the second molar were related to the first molar, first molar to first premolar, and first premolar to canine region. It can be immediately recognized that only values normalized to the bite forces permit meaningful comparisons. The findings of Hattori et al. [13], due to their significant larger magnitudes of the data, diverge systematically from those of the other studies. This discrepancy might be explained by variations in jaw opening, measurements of EMGs, and bite forces as well as by differences in force calculation. In particular, horizontal bite force directions were not controlled in the study of Hattori et al. [13]. Some principal characteristics, however, can be compared between maximum and submaximum constant force biting. Under maximum bites moving from molar to canine region [13], bite forces, muscle forces, and TMJ forces are reduced; thereby, the reduction is more pronounced for premolar than for canine biting. At submaximum constant bite forces, in contrast, TMJ and muscle forces increased incrementally when the bite force position changed from posterior to anterior. This behavior could consistently be observed for all investigated submaximum bite forces as confirmed by similar ratios of muscle and joint forces after normalization by the actual bite forces. This behavior expresses the fact that muscle efforts become increasingly inefficient and the joint increasingly loaded when the bite point moves anteriorly. During premolar bites, however, the anterior temporalis was higher loaded than the masseter, in contrast to an equal loading of both muscles at molar and canine bites. Similar tendencies were observed in the work of Hattori et al. [13]. This finding may be explained by different control strategies triggered by the SDAs representing equilibrium states which might be more susceptible to interferences than molar supported bites. Under such conditions, the temporalis, which rather controls force direction than force magnitude [8, 33], might be stronger activated to stabilize the jaw.

Table 2 Comparison of TMJ, bite, and cumulative muscle forces based on validated 3-D model calculations, between the current study and those of [10, 13, 20]

	Molar bites		Premolar bites		Canine bites	
	N	BF%	N	BF%	N	BF%
Current study						
Bite force	200	100	200	100	200	100
Joint force	125	63	155	78	190	95
Muscle force	240	120	274	137	315	157
[13]						
Bite force	600	100	450	100	200	100
Joint force	500	83	480	107	310	155
Muscle force	1250	208	1050	233	550	275
[10]						
Bite force	681	100	515	100	n.d.	n.d.
Joint force	315	46	359	70	n.d.	n.d.
Muscle force	≈740	≈109	≈780	≈151	n.d.	n.d.
[20]						
Bite force	n.d.	100	n.d.	n.d.	n.d.	n.d.
Joint force	n.d.	50	n.d.	n.d.	n.d.	n.d.
Muscle force	n.d.	≈ 160	n.d.	n.d.	n.d.	n.d.

Data are presented in Newton (N) and normalized with the bite forces (BF%). TMJ and muscle forces represent unilateral loads. For unilateral bites [10, 20], the mean of left and right side data are used. For the current study, the experimental data (n=10) for BF=200 N are considered

n.d. no data available, *BF* bite force

The experiments were conducted with insignificant changes in mandibular position during ES variations, and with strictly controlled vertical bite forces in the range of chewing forces. This allowed a direct comparison of all investigated bite positions. It may be objected that the experimental design does not resemble the balancing behavior during natural biting. However, during unilateral biting and chewing, comparable bilateral activity ratios of the jaw muscles occur [14]. These findings support the assumption that our results might also permit conclusions which are valid for biting and chewing tasks in the natural dentition.

There may be also some physiological limitations of this study:

(a) Muscle subunits show a differential contraction behavior [34, 35]. Hence, the real lines of action might somewhat vary from the reconstructed ones, due to the potential of the muscles to modify their direction of pull. This might negatively affect model calculations [36]. Furthermore, our recordings were conducted with an average molar separation of 4.5 mm. Compared to the natural intercuspation, this vertical distance changed the lines of action by about 2°. However, we do not believe that these small differences influenced the balancing behavior of the muscles relevantly.

(b) Periodontal mechanoreceptors were compromised by the experimental device. It is known that these receptors are directionally sensitive at low force levels, which may influence the bite force direction during the initial phase of the chewing cycle [37]. Most of these receptors, however, saturate at low bite force levels [38], and motor control might be dominantly influenced by muscle mechanoreceptors at higher force levels [39]. Therefore, we suppose that under the bite forces exerted in our static experiments the balancing behavior of the jaw muscles was not essentially influenced by the intraoral device. These assumptions are substantiated by the study results of Pröschel et al. [14].

(c) Force transmission between the dental arches is accomplished by multiple contact points in anteroposterior direction, which can be statically replaced by one single resultant force vector. Yet, for an intact intercuspation it is not known where in the occlusal plane this resultant force vector is located. Data with pressure-sensitive foils, however, refer to the midline between the first molars [40, 41]. With the present experimental device, the location of the resultant forces was set midline between the first molars, premolars, and canines. This might not exactly reproduce the transverse location of the resultant vectors in the natural intercuspation. Nevertheless, the balancing behavior of the motor system under changing dental support in anteroposterior direction seems to be modeled sufficiently.

The 3-D biomechanical model chosen in the present study was used to compute joint forces based on in vivo measurements extending a former 2-D model [21]. The results obtained with our model are based on various assumptions (*cf.* "Materials and methods" and "Appendix" sections). These factors might have contained errors on a subject- and/or task-oriented basis. It has also to be considered that pure model computations as well as calculations based on in vivo data are prone to measurement errors related to the collected biological parameters. In addition, it can be supposed that motor control applies variable control strategies during identical motor tasks, when experimental conditions change, as has recently been demonstrated [13, 28]. Therefore, detailed predictions of the motor behavior of individual subjects on the basis of model calculations should not be overestimated.

Considering the limitations of this investigation, it may be concluded that unilateral or bilateral molar biting with forces in the range of chewing forces significantly reduce TMJ and muscle loads in contrast to premolar or canine biting when identical bite forces are exerted and the jaw gap kept constant. The results are in line with findings of epidemiological [4] and experimental [1–3] studies that the ability of subjects without molars to comminute foods is reduced. Thus, our data provide a realistic quantitative biomechanical rationale for these observations.

Acknowledgments This investigation was supported by the Deutsche Forschungsgemeinschaft by grants SCHW 307/15-1 and STRU 675/1-1.

Conflict of interest The authors declare that they have no conflict of interest.

Appendix

Mathematical method

Force law

Muscle forces were specified according to the law $\overrightarrow{F}_i = P \cdot A_i \cdot \cos\alpha_i \{c\, U_{rel,i} + (1-c)\, U_{rel,i}^2\} \overrightarrow{e}_i$ ($\overrightarrow{F}_{\max,i} = P \cdot A_i \cdot \cos\alpha_i \overrightarrow{e}_i$). This equation extends the previously used law $\overrightarrow{F}_i = P \cdot A_i \cdot U_{\mathrm{rel,i}} \overrightarrow{e}_i$ [21] by a correction factor for the pennation angle α_i (for $\alpha \leq 15°: 0.97 \leq \cos\alpha \leq 1$) and parameter c characterizing the degree of nonlinearity between the muscle force and the relative electric muscle activity U_{rel}. This approach fulfills the following boundary conditions:

1. $F_i(U_{\mathrm{rel}}=0)/F_{\mathrm{max},i}=0$ (no electric activation corresponds to zero muscle force)
2. $F_i(U_{\mathrm{rel}}=1)/F_{\mathrm{max},i}=c+(1-c)=1$ (maximum muscle force at maximum activation)

Determination of parameters P and c

Due to model assumptions and measurement errors it cannot be expected that the balance of momentum of the muscle forces $\overrightarrow{F}_i$ and bite forces $\overrightarrow{B}_i$ with respect to the intercondylar axis (y-axis), to which the joint forces do not contribute, will be satisfied exactly. The torques of these forces with respect to the y-axis will rather sum up to a resulting error torque $\Delta M_y \neq 0$. In order to satisfy the balance of momentum exactly and, in addition, to gain an individual constant parameter set (P,c) for each subject (physiological properties of the muscles do not change under natural conditions for the individual subject), the following two-stage procedure was accomplished: In a first step, on the basis of 36 clenching tasks with bite force magnitudes ranging from 50 to 400 N, the best parameter set $(P,c)_{\mathrm{opt}}$, for which the objective function $f(P,c)=\sum_{n=1}^{36}\left(\Delta M_{y,n}/F_{\mathrm{res},n}\right)^2$ with $F_{\mathrm{res},n}=\left|\sum_{j=1}^{3}\overrightarrow{B}_{j,n}\right|$ reached a minimum value (minimization of the squared relative error torques), was computed via optimization. With the force law $F_i=f(P,c,U_{\mathrm{rel},i})$, all muscle forces would then be given by the measured EMG activities of the masticatory muscles. However, even for this optimal constant parameter set $(P,c)_{\mathrm{opt}}$ small error torques remain.

Principally, for the second step, two possibilities exist to continue:

1. Accepting small error torques ΔM_y due to inevitable (presumably minor) errors in measurement and/or assumptions, which are present even for the best parameter set. The advantage of this choice is that P_{opt} and c_{opt} are kept constant; the disadvantage is that no (exact) equilibrium can be achieved, i.e., the computed forces cannot represent the exact distribution of joint and muscle forces which balance the clenching forces.
2. Exactly fulfilling the equilibrium conditions by varying the parameter P (P_{var}), i.e., not using the constant P_{opt} computed by the optimization. The advantage of this approach is that the computed force distribution represents muscle and joint forces exactly balancing the bite forces. The disadvantage of this method is that P is variable. In the present work, option (2) was chosen. For c, the value of c_{opt} was maintained (Table 3).

Table 3 Equations used for the calculation of muscle and joint forces and footnote with used abbreviations

equilibrium conditions :

$$\sum\vec{F} = \sum_{j=1}^{3}\vec{B}_j+\vec{J}_r+\vec{J}_l+\sum_{i=1}^{12}\vec{F}_i=\vec{0}$$

$$\sum\vec{M} = \sum_{j=1}^{3}(\vec{r}_{B_j}\times\vec{B}_j)+(\vec{r}_{Jr}\times\vec{J}_r)+(\vec{r}_{Jl}\times\vec{J}_l)+\sum_{i=1}^{12}(\vec{r}_i\times\vec{F}_i)=\vec{0}$$

maximum muscle force and force law :

$$F_{max,i} = P\cdot A_i\cdot\cos\alpha_i \quad \text{with} \quad A_i=(1-p_i)\cdot V_i/l_{f,i}$$

$$F_i/F_{max,i} = c\cdot U_{rel,i}+(1-c)\cdot U_{rel,i}^2=f(U_{rel,i}) \quad \text{with} \quad U_{rel,i}=U_i/U_{max,i}$$

computation of P :

$$\sum M_y = P\cdot\sum_{i=1}^{12}A_i\cdot\cos\alpha_i\cdot(r_{z,i}\cdot f(U_{rel,i})\cdot\vec{e}_i\circ\vec{e}_x-r_{x,i}\cdot f(U_{rel,i})\cdot\vec{e}_i\circ\vec{e}_z) + \sum_{j=1}^{3}(r_{z,B_j}\cdot B_{x,j}-r_{x,B_j}\cdot B_{z,j})=0$$

$$P = \frac{\sum_{j=1}^{3}(-r_{z,B_j}\cdot B_{x,j}+r_{x,B_j}\cdot B_{z,j})}{\sum_{i=1}^{12}A_i\cdot\cos\alpha_i\cdot f(U_{rel,i})\cdot(r_{z,i}\cdot\vec{e}_i\circ\vec{e}_x-r_{x,i}\cdot\vec{e}_i\circ\vec{e}_z)}$$

total joint force :

$$\vec{J}_{total} = \vec{J}_r+\vec{J}_l=-\sum_{j=1}^{3}\vec{B}_j-\sum_{i=1}^{12}\vec{F}_i$$

$$\text{with} \quad \vec{J}_{r/l}=J_{x,r/l}\cdot\vec{e}_x+J_{y,r/l}\cdot\vec{e}_y+J_{z,r/l}\cdot\vec{e}_z$$

computation of the joint force components :

$$J_{x,r} = \frac{r_{y,Jl}\cdot J_{x,total}-\sum_{i=1}^{12}M_{z,i}-\sum_{j=1}^{3}M_{z,B_j}}{r_{y,Jl}-r_{y,Jr}} \quad ; \quad J_{x,l}=J_{x,total}-J_{x,r}$$

$$J_{z,r} = \frac{r_{y,Jl}\cdot J_{z,total}+\sum_{i=1}^{12}M_{x,i}+\sum_{j=1}^{3}M_{x,B_j}}{r_{y,Jl}-r_{y,Jr}} \quad ; \quad J_{z,l}=J_{z,total}-J_{z,r}$$

$$\text{with} \quad M_x=r_y\cdot F_z-r_z\cdot F_y \quad \text{and} \quad M_z=r_x\cdot F_y-r_y\cdot F_x$$

$$J_{y,r} = J_{y,total} \quad \text{and} \quad J_{y,l}=0 \quad \text{if} \quad J_{y,total}\leq 0$$

$$J_{y,l} = J_{y,total} \quad \text{and} \quad J_{y,r}=0 \quad \text{if} \quad J_{y,total}>0$$

$\vec{F}$	:	force vector	
$\vec{M}$	:	moment (torque) vector	
$\vec{B}_j$	:	measured bite forces	exerted on the mandible
$\vec{J}$	:	joint (reaction) force	exerted on the mandible
$\vec{r}$	:	vector from the origin of the coordinate system to the force application point ("lever arm")	
P	:	intrinsic muscle strength	
c	:	initial slope of the force law	
$\vec{F}_i$	:	actual force vector	of the i[th] muscle
$F_{max,i}$	:	maximum (static) force	of the i[th] muscle
$\vec{e}_i$	:	unit vector along line of action	of the i[th] muscle
A_i	:	physiological cross−section	of the i[th] muscle
α_i	:	pennation angle	of the i[th] muscle
p_i	:	fraction of tendinous tissue	of the i[th] muscle
V_i	:	(total) volume	of the i[th] muscle
$l_{f,i}$	:	fiber length	of the i[th] muscle
U_i	:	actual EMG activity	of the i[th] muscle
$U_{max,i}$	:	maximum EMG activity	of the i[th] muscle

Indices r and l refer to the right and left side of the mandible; indices x, y, z denote components with respect to the used coordinate system with unit vectors $\vec{e}_x$, $\vec{e}_y$, $\vec{e}_z$;
$\circ$: scalar (inner) product; $\times$: vector (cross) product.

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