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# Static balancing behaviour of the mandible

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The objective of this study was to investigate the mechanisms of physiological control of the craniomandibular system during force-controlled biting: in intercuspation, restricted by predetermined anatomic–geometrical conditions [i.e. biting in intercuspation (BIC)]; and on a hydrostatic system [i.e. auto-balanced static equilibrium of the mandible (BAL)], in which the mandible is balanced under unrestricted occlusal conditions. For 20 healthy subjects, the spatial positions of the condyles, the lower molars, and the incisal point were measured, and the electromyographic (EMG) activity of the musculus masseter and musculus temporalis anterior were recorded bilaterally, during force-controlled biting (50, 75, 100 N) on a hydrostatic device. The results were compared with those obtained during BIC. During BAL, the neuromuscular system stabilizes one condyle, so it behaves as a virtual fulcrum, and all available biomechanical degrees of freedom of the opposite side are used to achieve a bilaterally equal vertical distance between the upper and lower dental arches. The variability of the positions of the molars was significantly smaller than for the condyles. The EMG co-contraction ratios calculated for homonymous muscle regions revealed significant differences between BIC and BAL, specifically, greater symmetry during BAL with substantial asymmetry of approximately 25% remaining. In conclusion, the results revealed precise neuromuscular control of the position of the lower dental arch; this information might form the basis for interference-free tracking of the mandible in intercuspation under different conditions.

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Precise jaw movement is a basic component of physiological motor actions, such as chewing, speaking, and swallowing. To accomplish it, the motor cortex provides direct and indirect input to jaw-muscle neurons (1–6). Cell assemblies in the region of the medial bulbar reticular formation elicit semi-automatic movement by alternating contraction of jaw-opening and jaw-closing muscles (7). This so-called central pattern generator can be activated by appropriate input from specific higher centres (8), whereas peripheral receptors modify muscle performance by affecting the central pattern generator via direct pathways or by superimposition of jaw reflexes (9). In this context, feedback from periodontal mechanoreceptors (PMRs), muscle spindles (MS), and temporomandibular joint (TMJ) afferents is assumed to be crucial for the control of jaw movements (10–15). The neuronal connections between MS and PMR cell-somata in the trigeminal mesencephalic nucleus (16, 17) and, in particular, the convergence of their direct projections within the cerebellar cortex seem, moreover, to be the basis for appropriate processing of MS and PMR information during functional movement and in intercuspation (IC) (18–20). In contrast, the physiological significance of TMJ receptors in motor control of the craniomandibular system (CMS) seems insignificant, given its physiological range of motion (21), even though studies have revealed abundant sensory nerve supply to the tissues of the human TMJ (22–24). The kinematics of jaw movement and sensing of jaw position are, moreover, only slightly affected by PMR or anaesthesia of TMJ afferents (15). On the basis of these neurobiological data, it seems reasonable to assume major involvement of muscle afferents in the feedback control of functional jaw movement (15, 25).

In a recent study (26) the variability of condyle and incisal point (assumed to represent mandibular dentition) movement during repeated jaw closing on a preset target was analysed using uncontrolled manifold analysis (27). By use of this mathematical algorithm (which provides an estimate of control strategies during body movement) the amount of variability of the quantities examined in kinematic systems can be calculated. In three-dimensional CMS kinematics, this means that the variable which changes least between replicate movements is, explicitly, the controlled variable. The results revealed that during jaw closing, the incisal-point, rather than the condyles, was the precisely controlled variable. The authors concluded that the function of the TMJ may be primarily limited to three-dimensional biomechanical guidance during coordinated muscle co-contraction, enabling movement of the mandible into intercuspation via an interference-free route (26). These conclusions were supported by previous findings (15, 28).

In general, neuromuscular control strategies are analysed under static or dynamic conditions. Kinematic behaviour, electrical activity, or force distribution between the left and right sides of the jaws are common outcome variables (26, 29–31). Force and/or electromyographic (EMG) measurements are usually performed in intercuspation or in experimental occlusion and are monitored by the use of force transducers (32–34). These predetermined anatomic–geometrical measurements (i.e. the fixed distances between solid jaw structures) affect the co-contraction behaviour of the musculature. However, no data are available on the neuromuscular control strategies used by the CMS to achieve static equilibrium as soon as the structurally defined intercuspation is ended and movement capacity is unrestricted during bilateral force generation balancing the mandible. In addition, the sensorimotor effect on the different structures involved is completely unknown for free balancing conditions.

The objective of this study was to investigate the mechanisms of physiological control of the craniomandibular system during force-controlled biting: in intercuspation, restricted by the predetermined anatomic–geometrical conditions [i.e. biting in intercuspation (BIC)]; and on a hydrostatic system [i.e. autobalanced static equilibrium of the mandible (BAL)], in which the mandible is balanced under unrestricted occlusal conditions. The spatial positions of the condyles, the lower molars, and the incisal point were measured and the EMG activity of the musculus masseter (m. masseter) and musculus temporalis anterior (m. temporalis anterior) was recorded bilaterally. We hypothesized that the contraction behaviour of these muscles and the position of the mandible would significantly change between IC and the experimental balancing task of the mandible. The results might provide insight into strategies for neuromuscular control of the masticatory system.

## Material and methods

### Subjects

Twenty healthy subjects (10 male and 10 female; mean age: 24.7 ± 1.6 yr), were enrolled in the study. Exclusion criteria were painful temporomandibular disorders assessed according to the Research Diagnostic Criteria for Temporomandibular Disorders (RDC/TMD) (35), skeletal anomalies, or distinct malocclusion. Except for third molars, all subjects had full dentition.

The study was approved by the Ethics Committee of the University Medical Centre, Heidelberg (# S-537/2012). All subjects gave their written informed consent to participate in the study.

### Experimental set-up

The experimental set-up included use of two different devices for measurement of vertical and horizontal forces. The design resulted in a reproducible anteroposterior jaw position during experiments with a preset vertical jaw distance and a controlled vertical bite force. Two force sensors were integrated within an intraoral jaw-positioning device (Fig. 1A).

### Intraoral jaw-positioning device

By use of a face-bow, stone casts of the subjects were mounted on an articulator individually adjusted axiographically. Non-occluding plastic devices (3 mm Erkodur; Erkodent, Pfalzgrafenweiler, Germany) were fabricated for the upper and lower jaws, partly covering the lingual surfaces of all the teeth in the mandible and the palatal surfaces of the posterior teeth, including the palate, in the maxilla (Fig. 1A).

### Horizontal force measurement

By use of a dummy, the mandibular device was prepared with self-curing resin for insertion of a force sensor consisting of a modified metal ‘bearing pin’, equipped at half its height with four strain gauges (Hottinger Baldwin Messtechnik, Darmstadt, Germany) at 90° to each other (36). The transducer measured forces in two orthogonal directions (anteroposterior and lateral) relative to the occlusal plane. The signals were amplified by use of a measuring amplifier (MGCplus ML55B; Hottinger Baldwin Messtechnik, Darmstadt, Germany) and were displayed on a feedback monitor. The signals were digitized (sampling

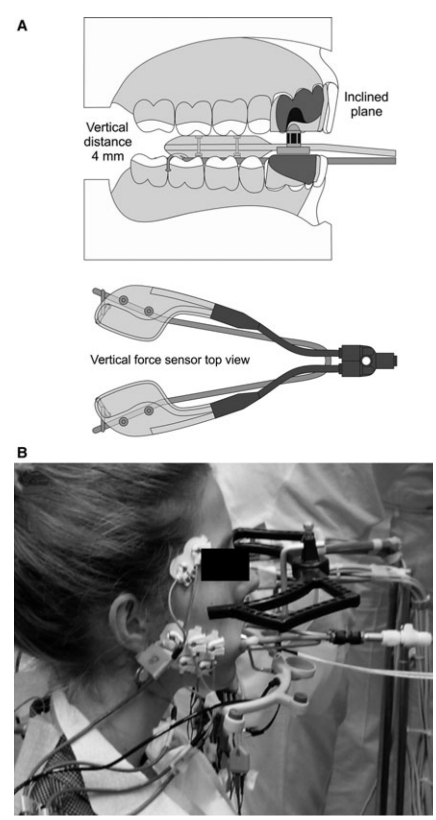


*Fig. 1.* (A) Schematic representation of the intraoral jaw-positioning device. (B) Participant equipped with all the measurement systems used in the study.

rate 1000 Hz) and recorded simultaneously with the EMG signals. The sensor provided information about displacement of the mandible as feedback for the subjects, ensuring stability of the position of the mandible in the horizontal direction during the experiments. An inclined plastic surface was attached to the upper device by use of self-curing resin, to guide the mandible by use of the bearing pin (Fig. 1A). This procedure enabled minor quasi-rotatory closing of the mandible, to compensate for small vertical discrepancies during biting on the pads at the different bite forces.

### Vertical force measurement

The vertical force component was measured by use of a hydrostatic system consisting of liquid-filled plastic pads (37) (components of a commercially available intraoral hydrostatic device; Aqualizer; Bausch, Köln, Germany) which were mounted on individually made paraocclusal attachments. The vestibular attachment was fixed by Rush anchors between the first and second lower molars (Fig. 1A). The pads were placed bilaterally between the rows of teeth in the premolar to molar regions. The closed-loop hydrostatic system of the bilaterally positioned pads enabled balancing of the mandible by adjusting the vertical distances between the jaws on both the left and right sides. This experimental design provoked the motor system to adjust static equilibrium involuntarily by using the intrinsic co-contraction repertoire of the neuromuscular system (37). Pressure measurement was accomplished by use of specific sensors integrated within the hydrostatic system. Because the pads were elastic, the applied bite force deformed them and reduced their vertical height, so the amount of liquid filling had to be adjusted by use of a small pump integrated within the hydrostatic system. This procedure resulted in fairly stable jaw separation of approximately 4 mm in the region of the first molars during the experiments. The pressure values were recorded simultaneously with the horizontal forces and the EMG data at a sampling rate of 1000 Hz.

### Electromyography

Four pairs of bipolar silver/silver chloride (Ag/AgCl) surface electrodes, 14 mm in diameter and with a centre-to-centre distance of 20 mm (Noraxon Dual Electrodes; Noraxon, Scottsdale, AZ, USA), were used to measure, bilaterally, the EMG activity of the anterior (Ma), medial (Mm), and posterior (Mp) parts of the m. masseter and of the m. temporalis anterior (Ta). The electrodes were placed parallel to the longitudinal axis of the muscles. Before application of the electrodes, the skin was cleaned with 70% ethanol. The common electrode was positioned on the neck above the seventh vertebra. The EMG signals were differentially amplified (EM 100; Biopac, Santa Barbara, CA, USA; frequency response 1–5000 Hz) and sampled at 1000 Hz simultaneously with the force signals. To obtain feedback signals from the m. masseter during the BIC tasks, the signals of the Mm electrodes were connected to a parallel circuit and recorded by use of an additional EMG amplifier. The rectified and averaged signals were displayed to the subjects on a feedback monitor. A horizontal guide on the display enabled adjustment of the specific EMG activity recorded by the feedback electrodes (Mm electrodes) at the different forces (50, 75, and 100 N) during the BAL experiments.

### Measurement of jaw position

Jaw position was recorded by means of an ultrasonic telemetric measurement system (JMA; Zebris Medical, Isny, Germany). The ultrasonic components were attached to the upper and lower labial surfaces of the teeth, using a paraocclusal device fixed with superglue. The accuracy of the ultrasonic measurement system was 0.01 mm for the range of mandibular displacements recorded in this study (26). The system recorded the spatial displacement of the mandible relative to a coordinate system determined by a reference plane parallel to the hinge axis–orbital plane. Positive $x$, $y$, and $z$ values represented anterior, cranial, and right displacements, respectively; negative values represented posterior, caudal, and left displacements, respectively (Fig. 2). The measurement points used for the analysis were:

(i) two condylar points on the hinge axis of the mandible, symmetrically located at a distance of 5.5 cm from the midsagittal plane (representing the right and left condyles, as virtually reconstructed by the measurement system's software);
(ii) two bilateral points on the buccal side of the first lower molars; and
(iii) one incisal point, defined between the lower first incisors.

Kinematic data were measured at a sampling rate of 75 Hz simultaneously with the EMG data.

### Measurement of chewing-side preference

During the appointment for impression-taking, the subjects were asked to chew a specified amount of wine gum three times. The side used twice or more was defined as the preferred chewing side. The subjects were also asked about their preferred chewing side. Before the test, no information about the reason for the test was given.

### Experimental procedure

The subjects performed two different feedback-controlled types of biting. One was performed by use of the hydrostatic system, which ensured BAL; the second task was performed in intercuspation (BIC). The subjects performed three trials at different forces (50, 75, and 100 N). Feedback was provided by a monitor, which displayed the vertical bite forces at the eye-level of the subjects. To ensure

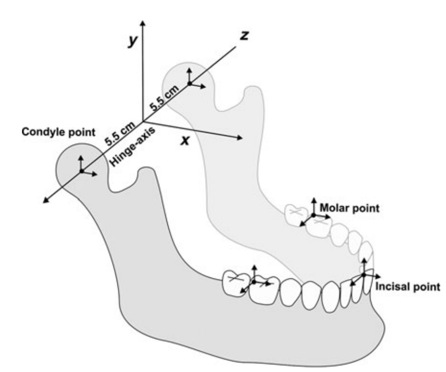


*Fig. 2.* Measurement points of the mandible and the defined reference planes.

reproducible horizontal positions of the mandible, in the first step the subjects were instructed to bite on the pads with the respective vertical bite force. Thereafter, they had to establish slight contact with the inclined surface of the maxillary device by means of the bearing pin, carefully moving the mandible in the anteroposterior direction and holding the achieved contact position with the least horizontal force possible. The subjects controlled this manoeuvre by means of the feedback monitor, which displayed the horizontal and vertical forces simultaneously. In this way, the subjects could precisely adjust, simultaneously, the horizontal jaw position and the vertical bite force on the pads. The bite force and position of the mandible had to be maintained for 3 s. After completion of BAL, the pads and the feedback sensor were removed and the subjects performed BIC. The bite force developed during this experiment was controlled by use of EMG feedback, as described above. The feedback threshold for the respective bite forces was determined from the mean values recorded during the BAL experiments. In this way, it was possible to replicate the biting tasks in intercuspation at forces almost identical to those used when the tasks had been performed with the pads incorporated. These tasks were also repeated three times for 3 s each. Finally, three maximum voluntary contractions (MVC) on cotton rolls were performed.

## Data analysis

As the first step of the kinematic analysis, the mean position during a 400 ms period from the middle of each 3 s trial was calculated; this represented the mandibular position during BAL. The spatial coordinates of the five mandibular measurement points investigated were computed as differences from IC.

For analysis of the reproducibility of the jaw positions during the BAL tasks, the absolute values of the spatial vectors of the condylar, molar, and incisal measurement points were computed for the replicates from each subject (38). The differences between the three replicate measurements were calculated and averaged for the sample (38). The result of this calculation served as a measure of the variability (i.e. the reproducibility) of the spatial displacement.

Data processing of EMG measurements was performed by use of the software MyoResearch XP Master Edition V 1.07 (Noraxon, Scottsdale, AZ, USA). The root-mean-square (RMS) values were computed and normalized to the MVC amplitudes. Mean and SD for a 400 ms period from the middle of the recordings were calculated for each trial and averaged for all the subjects.

In accordance with FERRARIO *et al.* (39), we investigated the symmetry of muscular co-activation of the right and left sides by calculating co-contraction ratios for every sample in the 400-ms period. The absolute co-contraction ratio differences (AR), and the side-specific co-contraction ratio differences (SR) (40) Ma right/Ma left, Mm right/Mm left, Mp right/Mp left, and Ta right/Ta left were calculated as follows:

$$\mathrm{AR} = \frac{1}{400}\sum_{i=1}^{400} r_i \qquad (1)$$

with the ratios $r_i$ defined as:

$$r_i \begin{cases} (1 - \mathrm{left/right}) & \text{if left} < \text{right} \\ (1 - \mathrm{right/left}) & \text{if right} < \text{left} \end{cases}$$

This computation provides absolute values for the asymmetric contraction behaviour. Maximum co-contraction is represented by a ratio equal to 0, whereas a minimum co-contraction is indicated by a ratio of approximately 1.

$$\mathrm{SR} = \frac{1}{400}\sum_{i=1}^{400} r_i \qquad (2)$$

with the ratios $r_i$ defined as:

$$r_i \begin{cases} (1 - \mathrm{left/right}) & \text{if left} < \text{right} \\ (\mathrm{right/left} - 1) & \text{if right} < \text{left} \end{cases}$$

Notation (2) was used as descriptive data analysis to provide information about side specificity by use of sign differences. The averaged side specificities for the individual subjects indicate the side preferences of the subject (i.e. which jaw side dominated the co-contraction pattern: positive values indicate dominance of the right side and negative values indicate dominance of the left side).

## Statistics

All statistical tests were performed using SIGMAPLOT 12.0 for WINDOWS (Systat Software, San Jose, CA, USA). Kolmogorov–Smirnov tests and normal probability plots were used to confirm normality of the data distribution.

The EMG differences as mean values, SD and AR for BIC and BAL, and the different forces were analysed using two-way repeated-measures ANOVA, adjusted using the Bonferroni correction for multiple comparisons.

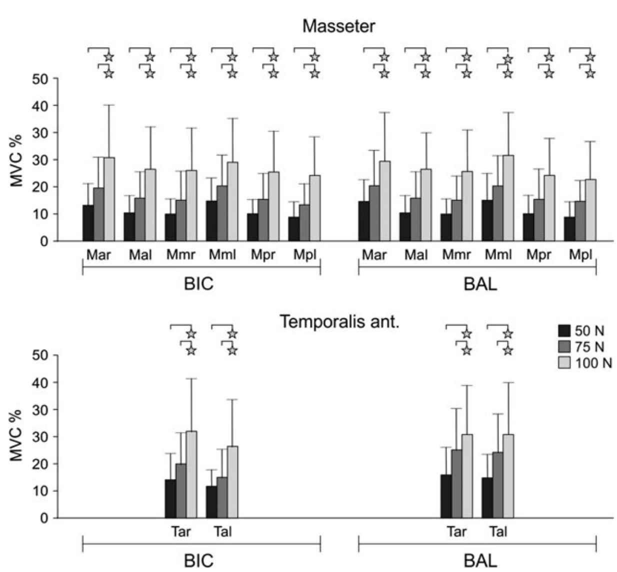


*Fig. 3.* Mean and SD of normalized electromyographic (EMG) activity of the right and left sides of the anterior (Ma), medial (Mm), and posterior (Mp) parts of the musculus masseter (m. masseter) and the musculus temporalis anterior (Ta). BIC, biting in intercuspation; BAL, auto-balanced static equilibrium of the mandible; Mar, m. masseter anterior right; Mal, m. masseter anterior left; Mmr, m. masseter medial right; Mml, m. masseter medial left; Mpr, m. masseter posterior right; Mpl, m. masseter posterior left; MVC, maximum voluntary contractions; Tar, temporalis anterior right; Tal, temporalis anterior left. Asterisks indicate significant ($P < 0.05$) differences between the experimental bite forces.

Side differences between the components of the displacement vectors (*x*, *y* and *z*) for the condyles and molars, and differences between reproducibility for condyles and molars, and for condyles and molars of identical jaw sides, were evaluated using Wilcoxon tests. The level of significance for all statistical tests was set to $P = 0.05$.

## Results

Mean RMS values of the MVC% normalized data for different bite forces were significantly different for both BAL and BIC tasks (Fig. 3). In contrast, significant differences between the two conditions could not be detected. Mean and SD of AR analysis revealed significant differences between BIC and BAL, however, as depicted in Fig. 4. The mean values obtained from the SR analysis are presented as descriptive statistics in Fig. 5.

For BAL, mean and SD of the displacements of the measurement points in the three measurement planes are presented in Fig. 6. The spatial displacement of the condyles and molars for the *x* and *y* components are plotted in Fig. 7. In comparison with the right side, the displacement of the left condyle was significantly larger for both the *x* and *y* components. For the left condyle, the horizontal displacement was significantly larger than the vertical displacement. Notwithstanding the differences between the spatial displacements of the sides of the condyles, the positions of the molars were indicative of bilateral equalization of the vertical distance between the upper and lower dental arches during balancing.

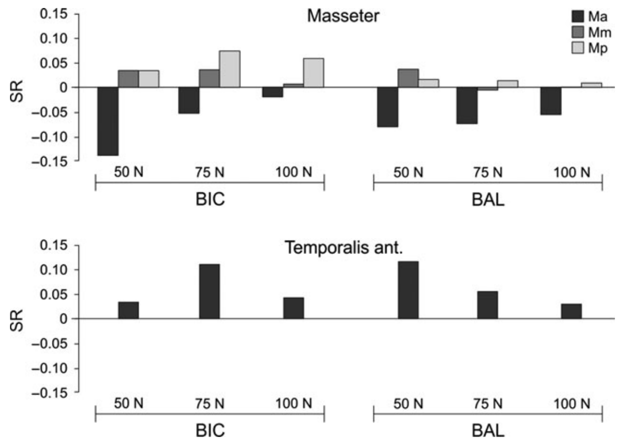


*Fig. 5.* Descriptive statistics of the averaged side-specific co-contraction ratio differences (SR) [notation (2)] of the anterior (Ma), medial (Mm), and posterior (Mp) parts of the musculus masseter (m. masseter) and the musculus temporalis anterior. BIC, biting in intercuspation; BAL, auto-balanced static equilibrium of the mandible. The SR represents the side preferences of the sample [i.e. which jaw side dominates the co-contraction pattern (positive values indicate dominance of the right side and negative values indicate dominance of the left side)]. Maximum co-contraction is indicated by an SR of 0, whereas minimum co-contraction is indicated by an SR of 1 or −1.

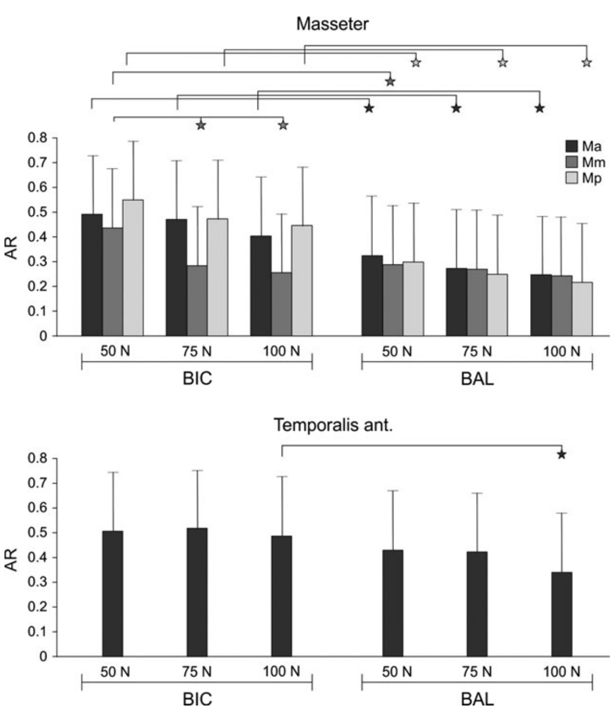


*Fig. 4.* Mean and SD of absolute co-contraction ratio differences (AR) [notation (1)] of the right and left sides of the anterior (Ma), medial (Mm), and posterior (Mp) parts of the musculus masseter (m. masseter) and the musculus temporalis anterior. BIC, biting in intercuspation; BAL, auto-balanced static equilibrium of the mandible. Maximum co-contraction is indicated by an AR of 0 whereas minimum co-contraction is indicated by an AR of 1. Asterisks indicate significant ($P < 0.05$) differences between the experimental bite forces and biting conditions.

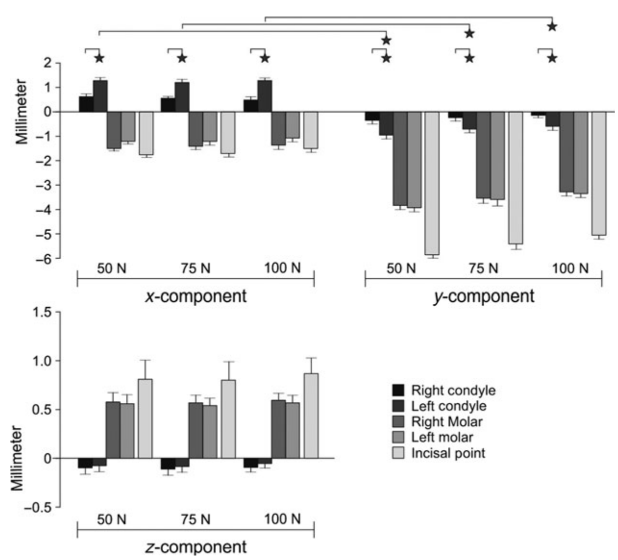


*Fig. 6.* Mean and SD of the displacements of the five measurement points from the reference position [i.e. intercuspation (IC)] during auto-balanced static equilibrium of the mandible (BAL) for the three different measurement planes. Asterisks indicate significant ($P < 0.05$) differences between the different measurement points and components.

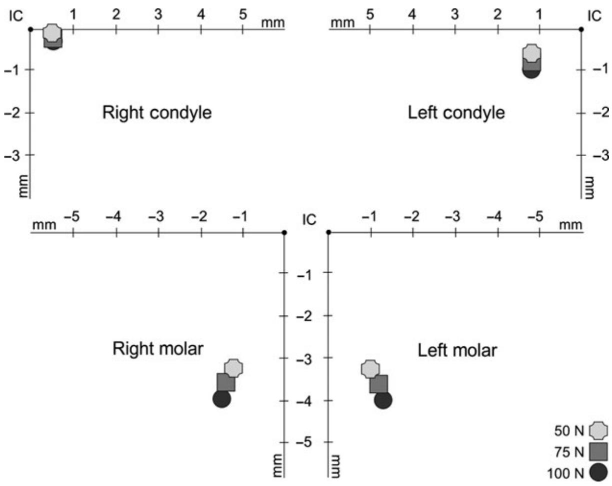


*Fig. 7.* Mean of the horizontal ($x$ component) and vertical ($y$ component) displacement components from the reference position [i.e. intercuspation (IC)] for the condyle and molar measurement points.

The reproducibility of the experimental positions was significantly better (i.e. the variability was smaller) for the position of the molars than for that of the condyles. For the right side, the reproducibility was also better for the position of the molars than for that of the condyles, but the difference was not significant (Fig. 8).

No differences were found between self-reported preferred chewing side and the results from chewing-side preference tests. Nine of the 20 participants preferred to chew on the right, whereas 11 preferred to chew on the left.

## Discussion

The purpose of this study was to analyse the neuromuscular control strategies of the CMS under force-controlled unrestricted balancing on a hydrostatic system and to compare the results with the contraction behaviour during BIC. Mandibular position changes during BAL compared with IC as reference were also analysed. The contraction behaviour of homonymous muscles and the position of the mandible were both

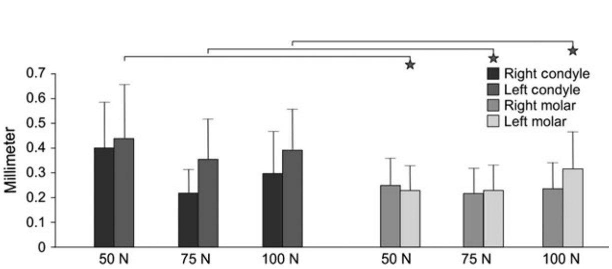


*Fig. 8.* Mean and SD of the reproducibility of condylar and molar special displacement from intercuspation during auto-balanced static equilibrium of the mandible (BAL). Asterisks indicate significant ($P < 0.05$) differences between reproducibility for the condylar and molar measurement points.

significantly different under the different experimental conditions. Therefore, the initially stated hypothesis can be accepted.

One of the main results of the study was the bilateral equalization of the vertical distance between the upper and lower dental arches during balancing, measured in the molar region. Most importantly, this bilateral equalization was observed under all bite-force conditions. With regard to initially reported conclusions from uncontrolled manifold analysis of jaw-closing movements (26), these new findings provide further evidence for the hypothesis that occlusion is the primarily controlled variable of the CMS, especially because, during simple jaw closing, the mandible also needs equal vertical interocclusal distances bilaterally to achieve intercuspation without interference. This reasoning is also supported by the fact that the variability during task replicates was smaller for the molar positions than for the condyle positions.

In contrast with the molar distances, the positional changes for the right and left condyles were significantly different from IC. The position of the right condyle was highly reproducible, close to the reference position in IC. In contrast, the position of the left condyle was indicative of more accentuated deviation from IC, characterized by a significantly larger component in the horizontal direction than in the vertical direction. The reproducibility of the position coordinates was also smaller than for the opposite condyle. In accordance with previous findings (26, 29), the results also showed that changes in the position of the condyle observed during balancing followed task-specific biomechanical demands. As stated previously (41, 42), this positional accuracy and adaptability of the fossa–disc–condyle complex is provided not only by the guidance of the anterior fossa incline but also, in particular, by an additional degree of freedom provided by the changes of the relative positions of the (sandglass shaped) articular disc between the condyle and the glenoid fossa (41). The condyles' positional changes might reflect a neuromuscular control strategy which uses a relatively stable condyle position on one side (as a quasi-stationary virtual fulcrum) and the contralateral condyle as compensatory element, passively meeting neuromuscular demands. In accordance with these considerations, in this study the direction of the small mandibular shift, caused by the asymmetric displacement behaviour of the condyles during BAL, was predominantly towards the right side. Obviously, most of the subjects used the right condyle as a virtual fulcrum whereas the left condyle used all the biomechanical degrees of freedom available to equalize the vertical distance between the upper and lower dental arches. This asymmetric behaviour during BAL might have been affected by the structural asymmetry of the TMJ (43), differences between bilateral muscle volumes (44), and/or neuromuscular compartmentalization (45, 36). It is also possible that, similarly to other neuromuscular preferences, for example handedness, a tendency of neuromuscular laterality might have been involved (46, 47); however, it seems that chewing-side preferences did not have a significant effect on the results of our study.

In accordance with previous studies, the AR revealed asymmetric co-activation of the homonymous muscle regions and changes of the ratios with increasing bite force during the different biting tasks (32, 48). During BAL, the AR revealed fairly identical asymmetric contraction behaviour of the three regions of the m. masseter measured. In comparison with BIC, this is indicative of better symmetry of the homonymous muscle regions during BAL. Nevertheless, substantial asymmetry of approximately 25% remained for the four homonymous muscle regions. This is additional evidence that asymmetric EMG values of jaw muscles during biting are a physiologically normal phenomenon, even though the mandible performs unrestricted balancing by means of a hydrostatic system.

The SR provided information on preferential left or right direction specificity of the bilateral co-contraction behaviour of homonymous muscles or muscle regions. The side preference (i.e. the muscle with the greater activation) was no different for BIC and BAL. For both experimental conditions, however, relevant opposite side dominance was observed for Ma and Ta (i.e. left-side preference for Ma and right-side preference for Ta). In contrast to BIC, a strictly progressive decrease of side preference with increasing bite force was observed during BAL. This result indicates that bite force is a crucial variable with regard to bilateral co-contraction behaviour. Surprisingly, this co-contraction pattern change had no significant effect on the kinematic performance of the mandible. This also might be an indicator of a neuromuscular control strategy that predominantly controls the mandibular position to furnish an interference-free route to IC, irrespective of the actual bite force generated.

The limitations of this experimental design must be considered. One limitation might be the complexity of the experimental design, which might have compromised the masticatory system to some extent (e.g. oral proprioception). Nevertheless, as far as we are aware, with the hydrostatic and kinematic measurement systems currently available, it was the most realistic approximation possible. Another limitation is the application of surface electrodes, which are less selective than intramuscular electrodes. However, they also provide significant information on changes of the general recruitment pattern of the three measured muscle sites under different conditions (49). In addition to other mechanoreceptors, feedback from PMR is relevant to control of the CMS (50, 51). It is likely that the different co-contraction ratios reported were biased by more vertical load transfer, caused by the elasticity of the sensor pads and their placement on the posterior dentition only. Furthermore, changes of jaw relation as a result of the slight side shifts (52) and task-dependent variations of the co-contraction strategy (53, 54) might have affected the differences between the asymmetric contraction patterns in BIC and BAL. It may nevertheless be assumed that the experimental design realistically reproduced unrestricted balancing of the mandible and the corresponding neuromuscular responses.

During unrestricted balancing of the mandible, the co-contraction behaviour of the jaw muscles studied is more symmetric than for their physiological asymmetric pattern in intercuspation. In addition, symmetric performance increases with increasing bite force, although kinematic variables do not reflect these changes of the muscular co-contraction pattern. During BAL, the neuromuscular system stabilizes one TMJ as a virtual fulcrum, whereas all available biomechanical degrees of freedom of the opposite condyle are used to achieve a bilaterally equal vertical distance between the upper and lower dental arches. In general, this strategy might form the basis of an interference-free route of the mandible to intercuspation under different conditions.

In conclusion, the results of this study provide further evidence in support of the hypothesis that occlusion is the primary controlled variable in human jaw motor control.

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