

Using sensitivity analysis to validate the predictions of a biomechanical model of bite forces

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Summary. Biomechanical modelling has become a very popular technique for investigating functional anatomy. Modern computer simulation packages make producing such models straightforward and it is tempting to take the results produced at face value. However the predictions of a simulation are only valid when both the model and the input parameters are accurate and little work has been done to verify this. In this paper a model of the human jaw is produced and a sensitivity analysis is performed to validate the results. The model is built using the ADAMS multibody dynamic simulation package incorporating the major occlusive muscles of mastication (temporalis, masseter, medial and lateral pterygoids) as well as a highly mobile temporomandibular joint. This model is used to predict the peak three-dimensional bite forces at each teeth location, joint reaction forces, and the contributions made by each individual muscle. The results for occlusive bite-force (1080N at M1) match those previously published suggesting the model is valid. The sensitivity analysis was performed by sampling the input parameters from likely ranges and running the simulation many times rather than using single, best estimate values. This analysis shows that the magnitudes of the peak retractive forces on the lower teeth were highly sensitive to the chosen origin (and hence fibre direction) of the temporalis and masseter muscles as well as the laxity of the TMJ. Peak protrusive force was also sensitive to the masseter origin. These result shows that the model is insufficiently complex to estimate these values reliably although the much lower sensitivity values obtained for the bite forces in the other directions and also for the joint reaction forces suggest that these predictions are sound. Without the sensitivity analysis it would not have been

possible to identify these weaknesses which strongly supports the use of sensitivity analysis as a validation technique for biomechanical modelling.

Introduction

Biomechanical modelling is an important technique in functional anatomy aiding both the basic understanding of form and function relationships, and also producing testable numerical predictions. Advances in computer software mean that producing complex simulations of biological structures has become relatively straightforward. The sophistication of these simulations is seductive however some experimental work, such as Hylander's recent work using strain gauges to measure the strain on the facial skeleton (Hylander and Johnson 2002), has shown that we must be careful accepting the results produced by such models.

There are a number of ways that confidence in the predictive capabilities of computer simulations can be increased. The first is to compare the parts of the simulation output that can easily be measured with values recorded experimentally. This can be for example the generated movement (Langenbach et al. 2002) or the metabolic energy consumption (Sellers et al. 2003). If the measured values match those predicted by the model then the likelihood that the other predictions are correct is increased. An additional approach that ideally should be considered in parallel with experimental verification is to test the model itself. One such method is sensitivity analysis (Campolongo et al. 2000). Such sensitivity analyses have been called for in previous biomechanical studies (e.g. Kramer 1999) but are rarely actually performed. In this technique the numerical values used as inputs to the model are treated as plausible ranges rather than single

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best estimate values. The model is then rerun a large number of times with input values sampled from these ranges and statistical analyses performed on the results to identify the input parameters that have the largest effect on the results. This forces the modeller to identify input parameters where there is a large degree of uncertainty and highlights the effects of this uncertainty on the outcomes. This information can then be used to identify flaws in the model.

A good area to investigate the value of sensitivity analyses is bite force modelling. Knowledge of the scale of forces applied to food particles by the occlusal surfaces of teeth is an essential component in understanding the mechanics of food reduction, but like other aspects of occlusal mechanics these forces are not easy to measure or to analyse. Forces derived from strain-gauge or other transducers mounted between the teeth (e.g. Pruim et al. 1978) attest only to the scale of forces which happen to be realised under a given experimental situation. Further, ethical questions arise in elicitation of maximum bite forces from humans. Various workers (e.g. Weijs 1980; Osborn and Barager 1985; Demes and Creel 1988; Koolstra et al. 1988; Van Eijden et al. 1988; Hannam and Wood 1989; Ossenberg et al. 1995) have produced biomechanical models of human and hominoid masticatory apparatus of varying complexity and have produced values for occlusal bite force broadly in line with experimentally derived values. More recent work (Langenbach et al. 2002) has illustrated the level of sophistication that can be achieved using commercial multibody dynamic analysis software as the simulation engine, and this approach has been adopted here.

Materials

Multibody dynamic modelling software requires the definition of the three types of data: the mass properties of the moving parts, the forces or movements applied to them and the constraints on their movement. The model was constructed using ADAMS (MDI Inc.) running on an Silicon Graphics Onyx 2 workstation (SGI, Mountain View, California). The only moving part is the mandible. The mass parameters of the jaw were calculated by ADAMS from its approximate shape and volume assuming a standard tissue density of 1050 kg/m³. This produced a mass of 0.34 kg and moment of inertia in the antero-posterior direction: 0.00027 kg/m², in the vertical direction: 0.0004/m² and in the buccolingual direction 0.00058/m². Products of inertia were assumed to be zero. The centre of mass was in the midline 4.5 cm below and 3.6 cm anterior to the TMJ. The forces were applied by the various muscles of mastication: the temporalis, the masseter, and the medial and lateral pterygoids. The muscles were treated as ‘working lines’ (Weijs 1980) arising and inserting at arbitrary points in the centre of their known areas of insertion as in Koolstra et al. (1988). All the muscles of mastication can be functionally subdivided, but as a first approximation they were left as single unit muscles. All combinations of all eight muscles (256 combinations) were in turn ramped to their maximum force value and the model allowed to stabilise. The value entered for the maximum force for each muscle (Table 1) was the product of the value of the intrinsic strength of the muscles of mastication

Table 1. Physiological cross-section and maximum force values for the masticatory muscles. All values but that for the lateral pterygoid are taken from Weijs and Hillen (1985). Lateral pterygoid values from McDevitt (1989).

Muscles	Physiological Cross Section (cm ²)	Maximum force (N)
Temporalis	11	410
Masseter	9	330
Medial pterygoid	6.7	250
Lateral pterygoid	1	37

(3.7 10⁶ Nm⁻², Weijs and Hillen 1985) and their physiological cross-section (Weijs and Hillen 1985, except for the lateral pterygoid, where the value was taken from McDevitt 1989).

The constraints on the model were provided at the teeth and temporomandibular joints. The TMJ is a complex joint and if it is modelled as a simple hinge it will only allow compressive (here, occlusal-surface-normal) bite forces. To allow shearing (here, occlusal-surface-parallel) forces to be produced a small amount of sliding movement needs to be allowed. The TMJs were therefore modelled as a pair of damped springs that were adjusted so that they allowed not only rotation but a few millimetres of sliding movement at maximum bite forces. The stiffness chosen was 100 000 Nm⁻¹, the damping factor was 100 Nsm⁻¹, and zero for the preload and original length. The force generated by the spring is related to these parameters via the following equation:

$$F = -D \frac{dl}{dt} - K \cdot (l - l_0) + F_0$$

Where:

- F is the force generated (N)
- D is the damping factor (Nsm⁻¹)
- t is the simulation time (s)
- K is the stiffness (Nm⁻¹)
- l is the calculated length of the spring (m)
- l_0 is the original length (m)
- F_0 is the preload (N)

The remaining component of the model was the food particle. This was conceived as a small object that resisted the movement of a particular tooth and was hence modelled as another damped spring of high stiffness (1 000 000 Nm⁻¹) with the other values as the TMJ. The damping values are required to prevent the model becoming unstable and oscillating.

The geometry of the skull and mandible was obtained as 3-D surface data by scanning both with a Model 3030 rapid high resolution laser scanner (Cyberware, Monterey, California). It was then converted into a simpler polygonal surface model using Surfacer (3-D Imaging International, Willebroeck, Belgium), and imported into AutoCAD (Autodesk, Guildford, UK) for addition of key landmarks (centre points of muscle attachments and teeth, centre of TMJ). Their co-ordinates for the skull and jaw used are given in Table 2 and the geometry of the model is shown diagrammatically in Figure 1. The resulting model was imported into ADAMS as a DXF file, and the active elements of the model were there attached to the geometry.

To find the maximum force in the five main orthogonal directions, the model was evaluated with 256 different muscle activation pattern (8 muscles – each muscle either maximally or zero stimulated), and with the food particle positioned between each

Table 2. Three-dimensional coordinates of model landmarks

Bone	Landmark	Functional description	Side	X (cm)	Y (cm)	Z (cm)	
Skull	Temporal fossa	Origin of temporalis	LHS	6.07	7.80	2.42	
			RHS	-6.07	7.80	2.42	
	Zygomatic arch	Origin of masseter	LHS	5.98	0.27	4.40	
			RHS	-5.98	0.27	4.40	
	Medial pterygoid plate	Origin of medial pterygoid	LHS	1.34	-1.00	2.80	
			RHS	-1.34	-1.00	2.80	
Lateral pterygoid plate	Origin of lateral pterygoid	LHS	2.04	-0.86	2.79		
		RHS	-2.04	-0.86	2.79		
Mandible	Coronoid process	Insertion of temporalis	LHS	4.59	-0.06	3.54	
			RHS	-4.59	-0.06	3.54	
	Lateral surface of angle	Insertion of masseter	LHS	4.70	-5.39	1.17	
			RHS	-4.70	-5.39	1.17	
	Medial surface of angle	Insertion of medial pterygoid	LHS	4.43	-4.22	0.56	
			RHS	-4.43	-4.22	0.56	
	Pterygoid fovea	Insertion of lateral pterygoid	LHS	4.32	-1.18	0.87	
			RHS	-4.32	-1.18	0.87	
	Condyle	Temporomandibular joint	LHS	4.81	0.02	0.76	
			RHS	-4.81	0.02	0.76	
	First Incisor	I1		LHS	0.15	-4.89	7.55
	Second Incisor	I2		LHS	0.67	-4.77	7.47
	Canine	C1		LHS	1.17	-4.59	7.24
	Third Premolar	P3		LHS	1.86	-4.61	6.58
	Fourth Premolar	P4		LHS	2.01	-4.48	6.05
	First Molar	M1		LHS	2.12	-4.32	5.06
Second Molar	M2		LHS	2.61	-4.03	4.26	
Third Molar	M3		LHS	2.80	-3.60	3.16	

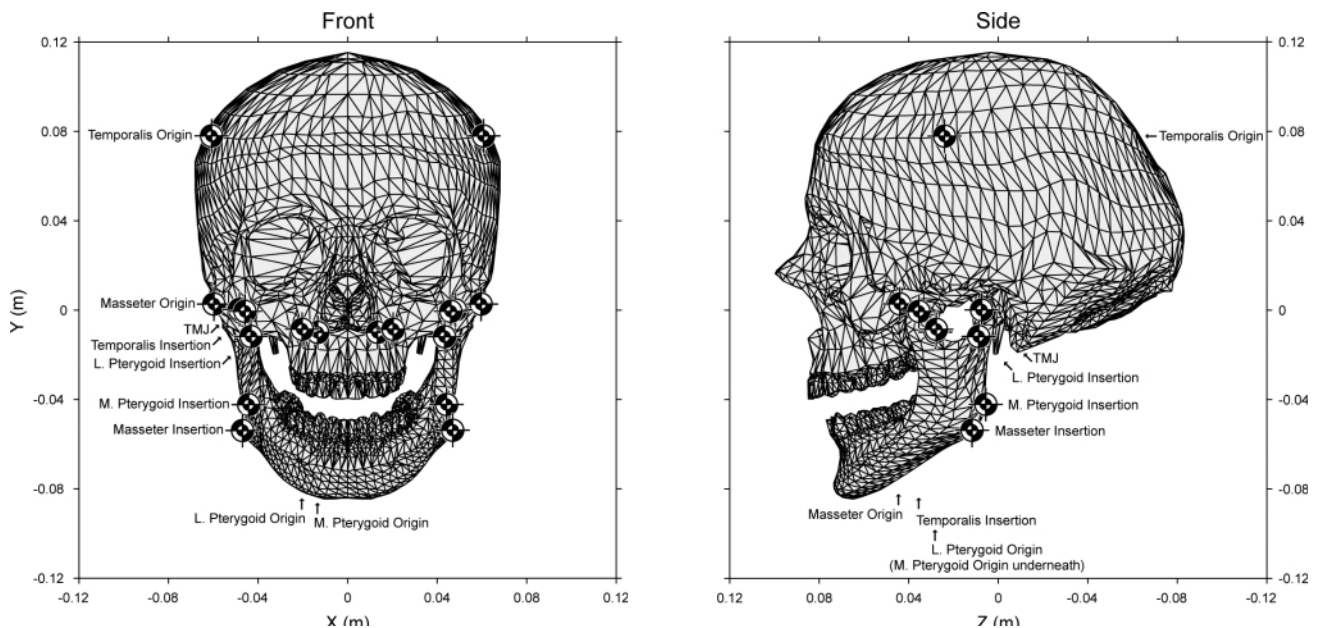


Fig. 1. A schematic view of the model showing the locations of the muscle attachment points and the temporomandibular joint.

tooth on the left-hand side. Thus in this model forces acting on the left hand side are considered ipsilateral to the food load and forces acting on the right hand side are considered contralateral.

For the sensitivity analysis the likely range of the model input parameters was estimated. These included the variations in the locations of muscle attachment points and the TMJ as estimated from examining the skull used in the model (Table 3). In addition

the stiffness values used for the TMJ and food particle constraint was allowed to vary over a wide range (TMJ from 25 000 to 400 000 Nm^{-1} and food particle from 250 000 to 4 000 000 Nm^{-1}) since these values were considered to be very uncertain. Values for muscle maximum forces were not included since these have a simple linear effect on any force predictions, and their individual contributions have already been identified by the multiple combi-

nation process described earlier. The mass properties of the mandible only effect the rate of movement of the jaw so do not effect the results obtained once the jaw has reached a stable position. One-At-a-Time (OAT) factor screening design sensitivity analysis was then performed (Campolongo et al. 2000). This type of analysis alters each parameter separately which has the advantage of being easy to implement and requires very much fewer simulation repeats than other designs. The disadvantage is that it does not allow factor interaction to be analysed. To achieve this the complete set of 256 simulations was repeated for each of 27 positional combinations (each of x, y and z at the minimum, middle, and maximum point in the range) for each of the nine locations, and at five points from the possible values of the stiffness for the TMJ and tooth constraint – a total of over 64 000 simulations. For a multifactorial design this number would increase geometrically. The food item was kept at M1 for all the sensitivity analysis runs since repeating this whole process a further eight times was felt to be unnecessary since the results for the different teeth were seen to follow a predictable pattern.

Results

Figure 2 shows the summary results from the 256 muscle activation combinations. As would be expected occlusal

Table 3. The coordinate ranges used in the sensitivity analysis

Muscle	X ± (cm)	Y ± (cm)	Z ± (cm)
Lateral Pterygoid Insertion	0.5	0.5	0.5
Lateral Pterygoid Origin	0.5	0.5	0.5
Masseter Insertion	1	1	2
Masseter Origin	1	1	2
Medial Pterygoid Insertion	0.5	0.5	0.5
Medial Pterygoid Origin	0.5	0.5	0.5
Temporalis Insertion	0.5	0.5	0.5
Temporalis Origin	1	2	2
TMJ Position	0.5	0.5	0.5

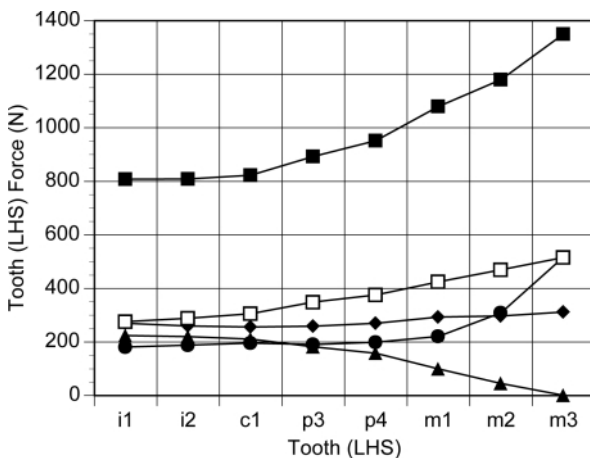


Fig. 2. The maximum force acting on the mandible at the left hand side lower tooth locations calculated by the model.
 ■ Occlusal Force, ● Protrusive Force, ▲ Retractive Force, ◆ Force to Left, □ Force to Right

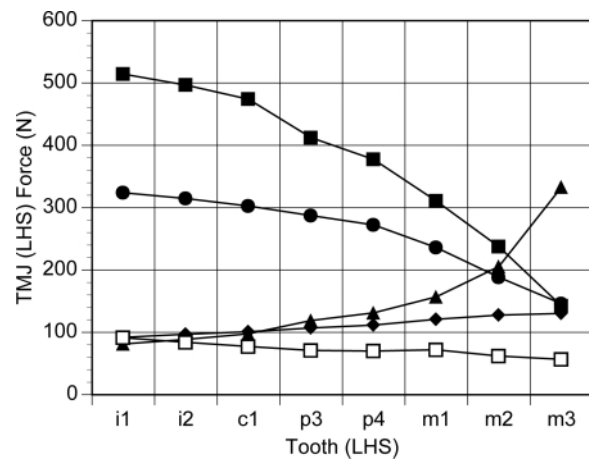


Fig. 3. The maximum force acting on the temporomandibular joint on the left hand side (ipsilateral to food) calculated by the model.
 ■ Occlusal Force, ● Protrusive Force, ▲ Retractive Force, ◆ Force to Left, □ Force to Right

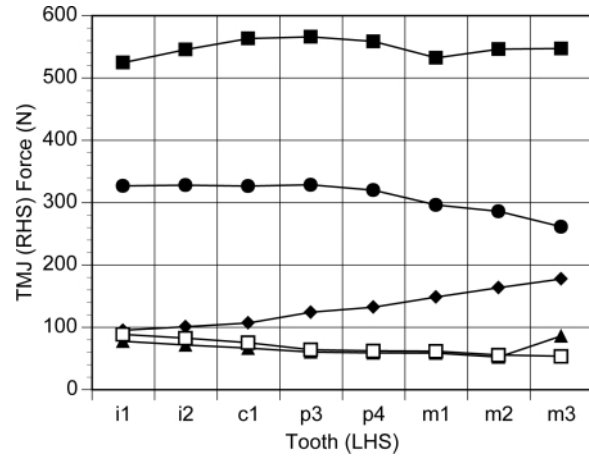


Fig. 4. The maximum force acting on the temporomandibular joint on the right hand side (contralateral to food) calculated by the model.
 ■ Occlusal Force, ● Protrusive Force, ▲ Retractive Force, ◆ Force to Left, □ Force to Right

forces, tending to close the jaw, are the largest – approximately three times larger than the shearing forces at each tooth location. All forces tend to increase proximally (posteriorly) with the exception of mandibular retraction. It can also be seen that for the distal teeth the muscles can move the teeth on the mandible more powerfully contralaterally than ipsilaterally to the food item and similarly, and that protrusion of the lower jaw is more forceful than retraction.

Also of interest is the reaction force generated at the temporomandibular joint itself. This is shown in Figures 3 and 4. There are large differences between the forces acting on the left hand side (ipsilateral to the food) and the right hand side. The joint reaction force is higher on the contralateral side in almost all cases and also varies relatively little with the location of the food particle.

Figures 5 and 6 show how the different muscles contribute to the force generated at the food particle on the left M1 and to the left TMJ reaction force. Normally, muscular contribution can be calculated from the total muscle force multiplied by the cosine of the angle between the angle of action of the muscle and the direction of interest. However because this model allows the mandible to move under the influence of the forces the individual muscle actions are not independent. The values reported are average contributions obtained by a stepwise multiple regression of all the muscle forces in

all 256 activation patterns against the force developed in the direction of interest. As would be expected the larger muscles dominate the force generation. For the force on the food particle both temporalis muscles are important for occlusion and the contralateral temporalis muscle has the greatest contribution for lateral movements. Protrusion is dominated by the masseters and retraction by the ipsilateral temporalis. The pterygoids are mainly involved in lateral movements. For the reaction force on the TMJ, the masseters have the biggest contribution to occlusive forces. Lateral movements are again

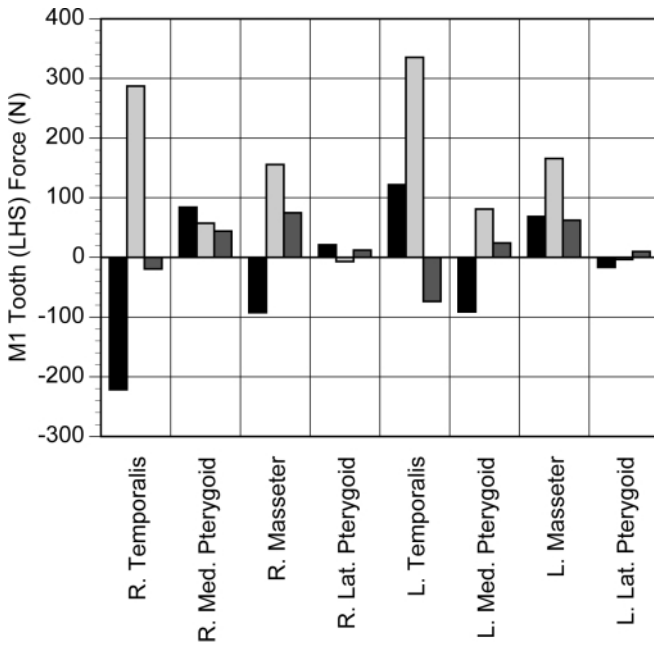


Fig. 5. The contributions of the individual muscles to the force generated on the left hand side first molar tooth. ■ Left, ■ Occlusion, ■ Protrusion

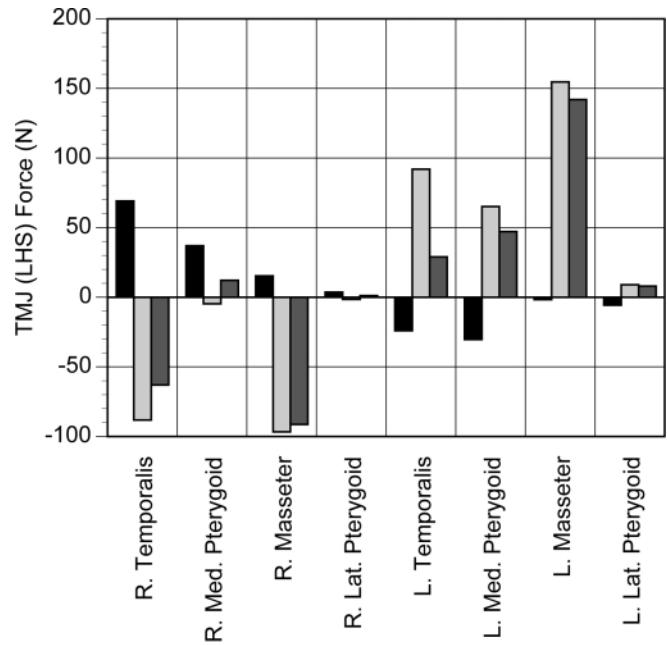


Fig. 6. The contributions of the individual muscles to the force generated on the left hand side temporomandibular joint. ■ Left, ■ Occlusion, ■ Protrusion

Table 4. The effects of altering the modelling parameters through the ranges from table 3 expressed as absolute ranges of the force (*minimum* to *maximum*) and percentage variation (*range/best estimate*). Values marked *** are where the *range/best estimate* is greater than 90%

	Peak Tooth Force (N)					Peak Left TMJ Force (N)				
	Left	Occlusion	Protrusion	Right	Retraction	Left	Occlusion	Protrusion	Right	Retraction
Best Estimate	293	1079	222	425	99	121	311	236	72	157
Temporalis Origin	247 to 341 32%	961 to 1124 15%	222 to 244 10%	363 to 483 28%	14 to 205 193% ***	84 to 147 52%	237 to 363 41%	221 to 305 36%	48 to 88 55%	141 to 183 27%
Temporalis Insertion	286 to 299 4%	1006 to 1156 14%	222 to 231 4%	413 to 437 6%	68 to 129 61%	100 to 139 32%	258 to 360 33%	221 to 284 27%	52 to 88 50%	134 to 177 28%
Masseter Origin	234 to 370 46%	1048 to 1086 4%	87 to 436 158% ***	330 to 528 47%	99 to 195 97% ***	111 to 154 36%	266 to 335 22%	210 to 247 16%	62 to 91 41%	91 to 204 72%
Masseter Insertion	233 to 365 45%	897 to 1233 31%	149 to 277 58%	336 to 521 44%	97 to 99 2%	111 to 158 39%	257 to 338 26%	165 to 291 54%	62 to 96 47%	134 to 167 21%
Medial Pterygoid Origin	260 to 321 21%	1057 to 1100 4%	167 to 296 58%	404 to 445 10%	99 to 109 10%	108 to 131 19%	292 to 329 12%	218 to 255 16%	65 to 77 17%	157 to 164 4%
Medial Pterygoid Insertion	270 to 311 14%	1028 to 1132 10%	186 to 263 34%	406 to 444 9%	99 to 99 0%	113 to 127 11%	306 to 316 3%	225 to 247 9%	65 to 78 18%	157 to 157 0%
Lateral Pterygoid Origin	289 to 295 2%	1079 to 1081 0%	210 to 232 10%	422 to 427 1%	99 to 99 0%	118 to 124 6%	306 to 315 3%	231 to 241 4%	69 to 74 7%	157 to 157 0%
Lateral Pterygoid Insertion	289 to 295 2%	1079 to 1082 0%	213 to 230 8%	421 to 428 2%	99 to 99 0%	118 to 123 4%	308 to 313 1%	232 to 239 3%	70 to 73 3%	157 to 157 0%
TMJ Position	283 to 303 7%	1018 to 1129 10%	167 to 262 43%	379 to 474 22%	85 to 112 28%	96 to 148 43%	276 to 348 23%	201 to 277 32%	55 to 84 40%	113 to 204 58%
TMJ Stiffness	257 to 303 16%	915 to 1173 24%	207 to 293 39%	330 to 464 31%	17 to 154 139% ***	104 to 121 14%	226 to 391 53%	198 to 245 20%	69 to 76 9%	144 to 185 26%
Food Constraint Stiffness	293 to 293 0%	1079 to 1080 0%	221 to 222 0%	425 to 425 0%	99 to 99 0%	121 to 121 0%	311 to 311 0%	236 to 236 0%	72 to 72 0%	157 to 157 0%

mainly caused by the temporalis and pterygoid muscles, and antero-posterior forces are dominated by the masseters.

Table 4 shows the effects of variations in the input parameters. The forces are the minimum and maximum forces obtained by varying a particular input parameter, and the percentage variation is calculated by dividing the range by the value calculated using the best estimates of the parameters. There are four large effects: the origin of the temporalis alters the estimate of the peak retractive force on a food particle at M1 from 14 to 205 N; the origin of the masseter alters the estimate of the peak retractive force on a food particle at M1 from 99 to 195 N and the peak protrusive force from 87 to 436 N; and the stiffness value used for the TMJ alters the peak retractive force from 17 to 154 N. Other effects are relatively small, with the choice of food constraint stiffness in particular having very little effect on the results.

Discussion

In order to evaluate the value of sensitivity analysis first the model needs to be tested by validation against other results elsewhere. The value for peak surface-normal bite force at M1 for this model is 1080 N which is rather larger than reported elsewhere. Pruim et al. (1978) experimentally recorded c. 730 N and other simulations reported values of 678 N (Koolstra et al. 1988), and 70 kg-force (approx 697 N) (Demes and Creel 1988). However a relatively large variation between studies is to be expected, as bite force is intimately linked to the physiological cross-section of muscles, which is very variable between individuals (Weijs and Hillen, 1985). Values from *in vivo* measurements may also be expected to be smaller, as real 'expressed' maxima for bite forces are unlikely to reach theoretical maxima.

In terms of qualitative predictions the finding that maximum bite forces increase posteriorly is 'common sense' and agrees with experimental strain-gauge studies by Pruim et al. 1980 as well as the findings of Koolstra et al. (1988) from their model. The asymmetry of retractive and protrusive shear forces predicted by this model appears to be a contrary result to that reported by Koolstra et al. (1988) and thus might tend to agree with Hylander's (1978) finding for incisal bite force direction. Greater protrusive shear would be the result expected from the anatomy of the masticatory muscles, since the muscle mass capable of exerting a retractive pull on the mandible is much less than that which can exert a protrusive pull. The left-right asymmetry of buccolingual shearing forces does not appear to have been previously reported, even qualitatively.

The TMJ reaction forces calculated are again in reasonable agreement with the work of other authors. Hylander (1975) showed that the joint reaction is greater on the

balancing side than on the working side. The magnitude of this difference varies depending on the tooth position of the food load. At the M1 level, the working side TMJ load is approximately half that on the balancing side which is somewhat lower than Smith's (1978) figure of 70 to 80%. The total TMJ reaction force is certainly highest when the load is on the incisors which agrees with Hylander's findings (1975, 1979).

When the results of the sensitivity analysis are considered a rather different picture is seen. The peak retractive force acting on the food particle is highly sensitive to the choice of temporalis origin. This large degree of variation means that this result is very insecure. The reason for this large effect is that over the range of values chosen the direction of action of the temporalis varies from almost vertical, with therefore no retraction component, to being angled posteriorly with a significant retraction component. This is an important finding since as well as identifying a major weakness it shows that the model could be significantly improved by subdividing the temporalis into functional units with differing muscle fibre directions. However, the direction of action of even the most posterior fibres of temporalis is reportedly largely vertical due to the fibres running across the front of the articular eminence at the root of the zygoma (DuBrul 1980) so that changing the fibre directions in the body of the muscle may not be the answer. The peak retractive force is also sensitive to the choice of stiffness coefficient in the TMJ. Once again this is probably because a lax constraint allows more movement of the mandible and this allows the direction of action of the temporalis muscle to change once again. The effect of the masseter origin is interesting – moving the origin along the zygomatic arch converts the muscle from generating a protractive force at M1 when the origin is anterior to the tooth to generating a retractive force when it is posterior again casting doubt on the reliability of AP force prediction in this model. Fortunately the other results are much more secure varying relatively little given the size of the variations in input parameters. It is reassuring that the food constraint stiffness value has so little effect since this value is largely arbitrary. Overall the results of the sensitivity analysis are extremely encouraging and allow us to estimate the reliability of the various results from the model: peak occlusive forces are highly reliable; peak lateral forces somewhat less so; and peak AP forces on the food particle show large variability in possible values.

In general these results strongly support the use of sensitivity analysis when reporting the results of biomechanical models. The one-at-a-time approach demonstrated here will underestimate sensitivity effects since it only looks at factors individually. It is almost certain that some factors will potentiate the effects of other factors and a multifactorial approach is to be preferred. However any form of sensitivity analysis requires a large number of repeats and computational considerations may make this impossible. Large numbers of repeats also requires that the modelling environment can be automated. This is not

always possible with highly interactive systems since they tend to be user interface driven. Even with batch based systems it can be difficult to automate the sampling of values from ranges. However as computational power increases, and especially since sensitivity analyses can be run in parallel on multiple processors, it is fast becoming an essential part of any modelling based piece of research.

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References

- Campolongo F, Saltelli A, Sørensen T, Taratola S (2000) Hitchhikers' guide to sensitivity analysis. In: Saltelli A, Chan K, Scott EM (Eds) *Sensitivity Analysis*. Wiley: Chichester, pp 15–47
- Demes B, Creel N (1988) Bite force, diet and cranial morphology of fossil hominids. *J Hum Evol* 17: 657–670
- DuBrul EL (1980) *Sicher's oral anatomy*. St. Louis: Mosby
- Hannam AG, Wood WW (1989) Relationships between the size and spatial morphology of human masseter and medial pterygoid muscles, the craniofacial skeleton, and jaw biomechanics. *Am J Phys Anthropol* 80: 429–445
- Hylander WL (1975) The human mandible: lever or link? *Am J Phys Anthropol* 43: 227–242
- Hylander WL (1978) Incisal bite force directions in humans and the functional significance of mammalian mandibular translation. *Am J Phys Anthropol* 43: 227–242
- Hylander WL (1979) An experimental analysis of temporomandibular joint reaction force in macaques. *Am J Phys Anthropol* 51: 433–456
- Hylander WL, Johnson KR (2002) Functional morphology and *in vivo* bone strain patterns in the craniofacial region of primates: beware of biomechanical stories about fossil bones. In: Plavcan JM, Kay RF, Jungers WL, van Schaik CP (Eds) *Reconstructing behaviour in the primate fossil record*. Kluwer Academic/Plenum Publishers: New York, pp 43–72
- Koolstra JH, Van Eijden TMGJ, Weijs WA, Naeije M (1988) A three-dimensional mathematical model of the human masticatory system predicting maximum possible bite forces. *J Biomechanics* 21: 563–576
- Kramer PA (1999). Modelling the locomotor energetics of extinct hominids. *J Exp Biol* 202: 2807–2818
- Langenbach GEJ, Zhang F, Herring SW, Hannam AG (2002) Modelling the masticatory biomechanics of a pig. *J Anat* 201: 383–393
- McDevitt WE (1989) *Functional anatomy of the masticatory system*. London: Butterworth
- Osborn JW, Baragar FA (1985) Predicted pattern of muscular activity during clenching derived from a computer assisted model: symmetric bite forces. *J Biomechanics* 18: 599–612
- Ossenberg NS, Steele SS, Howes J. (1995) Occlusal load and temporomandibular reaction forces in prehistoric Eskimos vs. modern Eurasians. *Am J Phys Anthropol Suppl* 20: 164 (Abstract)
- Pruim GJ, Ten Bosch JJ, de Jongh JJ (1978) Jaw muscle EMG-activity and static loading of the mandible. *J Biomechanics* 11: 389–395
- Sellers WI, Dennis LA, Crompton RH (2003) Predicting the metabolic energy costs of bipedalism using evolutionary robotics. *J Exp Biol* 206: 1127–1136
- Smith RJ (1978) Mandibular biomechanics and temporomandibular joint function in primates. *Am J Phys Anthropol* 49: 341–349
- Van Eijden TMGJ, Klok EM, Weijs WA, Koolstra JH (1988) Mechanical capabilities of the human jaw muscles studied with a mathematical model. *Archs Oral Biol* 33: 819–826
- Weijs WA (1980) Biomechanical models and the analysis of form: a study of the mammalian masticatory apparatus. *Am Zool* 20: 707–719
- Weijs WA, Hillen B (1985) Cross-sectional areas and estimated intrinsic strength of the human jaw muscles. *Acta Morphol Neerl-Scand* 23: 267–274

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