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Interactions between jaw-muscle recruitment and jaw-joint forces in *Canis familiaris*

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INTRODUCTION

It has often been assumed that maximum bite forces are produced by fully recruiting all the jaw-adductor muscles (Buckland-Wright, 1978; Greaves, 1983; Herring, 1985; Hiiemae & Crompton, 1985; Weijs, 1981). In man, however, it has been shown that subjects can increase their maximum bite force following the application of local anaesthetic to the tissues surrounding the teeth (O'Rourke, 1951; Orchardson & MacFarlane, 1980). Maximum voluntary bite force is, therefore, normally constrained by intra-oral afferent activity. This paper describes the jaw-adductor muscle activity patterns in the domestic dog (*Canis familiaris*) during mastication and bone crushing and shows that an additional constraint is placed upon the recruitment of the jaw-adductor muscles by interactions between muscle activity and jaw-joint forces.

Previous attempts to record *in vivo* jaw-adductor muscle activity in the dog comprise two electromyographical studies (Leibman & Kussick, 1965; Vitti, 1965). The work of Leibman & Kussick was not, however, designed as a detailed study of masticatory muscle activity and involved only one pair of electromyographic electrodes in the temporalis muscle. The work of Vitti was more detailed but employed coaxial needle electrodes which record muscle potentials only from a small area of muscle and therefore exclude significant portions of the muscles of mastication. One finding common to both of these studies, and of some importance, is that working-side muscle activity (temporalis in Leibman & Kussick; temporalis and masseter in Vitti) is reported to be greater than balancing-side muscle activity during mastication and bone crushing.

MATERIAL AND METHODS

Electromyography

To determine the magnitude and patterns of muscle activity during mastication and bone crushing, electromyographic activity from the masseter, temporalis and medial pterygoid muscles was recorded from dolichocephalic shepherd-mix dogs weighing 30–45 kg.

The dogs were initially trained for a period of one to six months to be handleable and to accept food from the investigator in the laboratory. Feeding behaviour was unrestrained and typically the dogs fed in the prone position holding meat and bones in their forepaws while using their carnassial teeth to masticate meat or bite on bones. No attempts were made to introduce additional variability into this behaviour since

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the animals frequently alternated food items between their right and left toothrows. Once the animals were accustomed to feeding in the laboratory, a leather harness designed to support an electromyographic telemetry transmitter was fitted to the animal daily for a period of one to three hours. Several weeks of daily wearing were needed to adapt the animal to the telemetry harness.

Surface electromyography was chosen for many of the temporalis and masseter electromyographic recording sessions so that as large an area of muscle as possible could be sampled. Since both of these large muscles are underlaid by bone, the potential for electromyographic crosstalk from adjacent muscles is small. Twenty recording sessions from 4 adult animals with good dentitions (3 females, 1 male, ages unknown) were analysed during bone crushing and masticating raw meat. Sixty eight different electrode placements (34 temporalis, 34 masseter) resulted in the analysis of 78 cycles during the mastication of meat and 137 bites during bone crushing. Surface electromyographic activity was recorded from the masseter and temporalis muscles using Beckman Miniature Skin Electrodes (8 mm contact diameter) with an impedance of less than 25 Ω at 1000 Hz (Fig. 1). Electromyographic activity was recorded through the use of a four-channel telemetry system (Biosentry Telemetry Model 4200A) incorporating a 1 kg transmitter strapped to the animal's back and a receiver. The system has a bandpass of 20–400 Hz and an input impedance of K500 Ω.

To quantify surface electromyographic activity, the signal was full-wave rectified and low-pass filtered (i.e. integrated) for each channel (time constant = 0·2 sec). The electromyographic output during each bite was then converted to a percentage by dividing by the maximum integrated electromyographic value for that electrode during the recording session. Standardisation of the electromyographic output in this manner should compensate for differences among electrodes and differences in electrode placement (Zuniga, Truong & Simons, 1970). Except for very low electromyographic amplitudes, (less than 20% of the maximum) which were not used in the analysis, each individual peak of the filtered electromyographic signal was determined by visual inspection to correspond to one jaw closure (i.e. bite). This correspondence was confirmed by analysis of simultaneous split-screen videotape recordings during biting which showed the dog's head including the lower jaw in one half of the screen and an oscilloscope display of jaw-muscle electromyographic activity in the other half of the screen.

To verify surface electromyographic recordings and examine intramuscular recruitment patterns, 20 additional recording sessions were carried out in five animals (4 female, 1 male) employing fine-wire indwelling electrodes inserted into various portions of the temporalis, masseter and medial pterygoid muscles. The dogs were initially lightly anaesthetised with a mixture of halothane, nitrous oxide and oxygen for 5–10 minutes while wire electromyographic electrodes were inserted into the jaw muscles with needles (Basmajian, 1978). The animals were then allowed to recover for 30–45 minutes before feeding; at this time they walked freely about the laboratory and showed no signs of discomfort or uncoordination. Recording sessions typically lasted 1–4 hours.

The electromyographic electrodes consisted of 0·076 mm stainless steel wire (A-M Systems) with 1 mm bared tips and an impedance of 17 Ω at 1000 Hz. Four portions of the temporalis muscle were examined as shown in Figure 1: the anterior temporalis (17 electrodes); the middle temporalis (11 electrodes); the posterior medial temporalis (14 electrodes) and the posterior lateral temporalis (3 electrodes). Sixty three cycles during the mastication of meat and 80 bites during bone crushing were recorded and analysed.

Activity within three portions of the masseter muscle of five dogs was examined

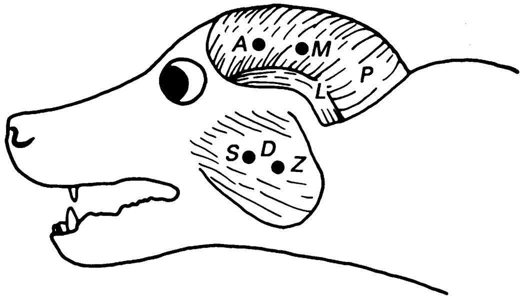

Fig. 1. Lateral view of a dog's head showing the location of electromyographic electrodes. Dots represent surface electrode positions; letters represent wire electrode positions. *A*, anterior temporalis; *M*, middle temporalis; *P*, posterior medial temporalis; *L*, posterior lateral temporalis; *S*, superficial masseter; *D*, middle masseter; *Z*, zygomatico-mandibularis.

using 18 electrodes during 96 meat masticating cycles and 70 bone-crushing bites. The masseter electromyographic electrodes were placed as shown in Figure 1 in the superficial masseter (2 electrodes), the middle masseter (10 electrodes) and the deep masseter (zygomatico-mandibularis) muscle (6 electrodes).

Electromyographic activity within the medial pterygoid muscle was examined in two dogs using 10 electrodes during 35 bone crushing bites. Electrodes were inserted by palpating the inferior border of the angle of the mandible just medial to the angle of the mandible.

Unlike the surface electromyographic recordings, electromyographic activity recorded with indwelling wire-electrodes was not quantified. Electromyographic output was initially recorded on tape and later played back onto chart paper so that electromyographic amplitudes during mastication and bone biting could be visually compared between portions of the muscles.

Jaw-joint loading during muscle simulation

To determine the range of potential jaw-joint forces that could be produced by various combinations of jaw-muscle activity and bite-point location, bone strain adjacent to the jaw joint was recorded during simulated biting and correlated with bone strain recorded during jaw-joint manipulations.

A ligamentous preparation was made by removing the skin, muscle and soft tissues from a fresh adult male dolicocephalic dog head while leaving the joints and ligaments intact. A single-element strain gauge (Micro-Measurements SA-06-125BT-120) was moisture-proofed (Micro-Measurements M-coat G and M-coat D) and bonded to the zygomatic arch with its long axis rotated 45 degrees laterally (counter-clockwise) from the midline (Fig. 8*h*). Implantation of the strain gauge in this orientation ensures a uniformly smooth area of bone on which to bond the strain gauge and positions the gauge on a region of the zygomatic arch overlying the mandibular condyle. The strain gauge implantation site was prepared by first abrading the bone surface with silicon–carbide paper, then neutralising it (Micro-Measurements neutraliser) and allowing it to air dry. A catalyst (Micro-Measurements 200-catalyst) was then applied to the strain gauge and allowed to dry for one minute. Methyl cyanoacrylate adhesive (Permabond 910) was applied to the strain gauge and it was pressed onto the bone with finger pressure for two minutes. The mandibular condyle was then manipulated to simulate various loading conditions while bone strain was recorded on chart paper.

Compressive condylar loading was produced by holding the animal's skull in one hand and pushing the lower border of the mandible and therefore the mandibular condyle directly dorsally with the other hand. Tensile condylar force was produced by holding the animal's skull in one hand and pulling the lower border of the mandible and mandibular condyle ventrally. During the manipulations the lateral pole of the mandibular condyle was closely observed to ensure that medial or lateral displacements of the condyle did not occur. Bone strains recorded during these manipulations were then compared to those recorded while simulating masseter and temporalis muscle activity combined with various bite-point locations.

Masseter muscle activity was simulated fifty times by grasping the skull with one hand and placing the thumb of the other hand under the ventral border of the mandibular body close to the insertion of the superficial masseter muscle and the fingers along the dorsal edge of the anterior portion of the zygomatic arch. Pressure applied between these two points approximates the line of action of the superficial masseter muscle and was used as a crude simulation of the direction of masseter muscle force.

Temporalis muscle activity was simulated by attaching a wire to the middle of the dorsal edge of the coronoid process. Temporalis muscle activity was then simulated fifty times by holding the skull in one hand and pulling the wire either dorsally or posterodorsally towards the temporal fossa. This pulling action simulates the direction of forces produced by portions of the temporalis muscle. During these muscle-force simulations, a 2·5 cm cube was placed at the canine or carnassial teeth to produce a rigid bite point, and bone strain from the dorsal surface of the zygomatic arch was recorded. It is important to emphasise that these simulations were used only to approximate the range of possible interactions between jaw-adductor muscle activity, bite-point location and jaw-joint loading. The inherent variability in these simulations was considered to be desirable since the goal was to determine the range of bone strains that could potentially be generated by jaw-adductor muscle activity.

Jaw-joint loading during muscle stimulation

To approximate more closely the *in vivo* relationship between jaw-muscle activity, bone strain on the zygomatic arch and jaw-joint forces, individual jaw muscles were electrically stimulated while bone strain from the zygomatic arch was recorded and subsequently correlated with manipulations of the mandibular condyle. Two dogs were anaesthetised with pentobarbitone sodium (Nembutal, 60 mg/kg i.v.) and a horizontal incision was made through the skin and temporalis fascia along the dorsal border of the zygomatic arch from the centre of the arch to its posterior end. The small portion of the temporalis muscle that takes its origin from the zygomatic arch was then reflected and the surgical field cleared with thrombin. The periosteum overlying the dorsal surface of the zygomatic arch was then scraped away and the bone was degreased and allowed to air dry. A rosette strain gauge (Micro-Measurements WA-06-030WR-120) was then bonded to the dorsal surface of the zygomatic arch overlying the mandibular condyle with methyl cyanoacrylate adhesive (Fig. 2).

The temporalis and masseter muscles were then directly stimulated with needle electrodes (138 stimulations; Grass model S48; 1 sec pulse, 50–150 V) individually and together to produce a fused tetanus. The temporalis-stimulating electrodes were positioned approximately 2 cm and 4 cm caudal to the external frontal crest and approximately 1 cm lateral to the midline for the anterior electrode and 1·5 cm lateral to the midline for the posterior electrode. The temporalis muscle was stimulated 67 times with the bite block at the ipsilateral canine teeth (9 stimulations), the ipsilateral carnassial teeth (24 stimulations), the contralateral canine teeth (5 stimulations), and

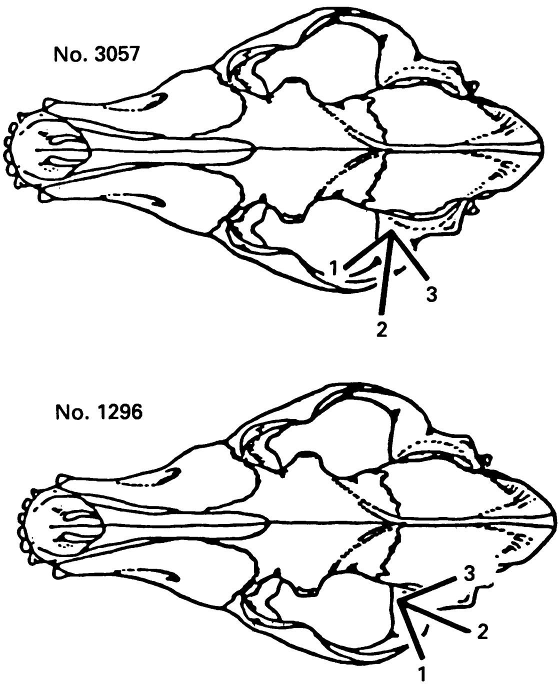

Fig. 2. Dorsal views of the skulls of Dogs 3057 and 1296 showing the orientation of the strain gauges bonded to the dorsal surface of the left zygomatic arch. Individual elements of the rosette strain gauge are numbered 1, 2 and 3.

the contralateral carnassial teeth (29 stimulations). Masseter-stimulating electrodes were positioned approximately 1 cm ventral to the zygomatic arch and 1·5 cm apart in the middle of the muscle. The masseter muscle was stimulated 51 times with bite points at the ipsilateral canine teeth (10), the ipsilateral carnassial teeth (23), and the contralateral carnassial teeth (18). In 20 further stimulations the right and left masseter and temporalis muscles were simultaneously stimulated, 10 with the bite point at the canine teeth and 10 at the carnassial teeth. Muscle stimulation was determined by palpation to be confined to the stimulated muscle(s) and the overlying facial muscles. During these muscle stimulations, bone strain was recorded from the dorsal surface of the zygomatic arch and subsequently correlated with manipulations of the mandibular condyle. The animals were killed following the muscle stimulation with an overdose of sodium pentobarbitone.

Bone-strain data from all experiments were used to compute the magnitude and orientation of the maximum principal strain, minimum principal strain and maximum shear stress. In addition to these calculations, geometrical constructions of the data as Mohr's circles were plotted. A Mohr's circle consists of a pair of orthogonal axes with the maximum and minimum principal strains plotted on the horizontal axis and one half the shear strains ($\gamma/2$) plotted on the vertical axis. A circle is then constructed on the horizontal axis at the midpoint between the maximum and minimum principal strains. The convention of Mohr's circle is that principal strain values in the positive portion of the horizontal or (ϵ) axis represent tensile strain. Shearing strain in the clockwise direction is represented above the horizontal axis and shearing strain in the counter-clockwise direction is plotted below the x-axis. The advantage of constructing a Mohr's circle as opposed to simple descriptive statistics is that it can then be used to determine the magnitude and type of strain in any direction within the plane being considered by the coordinates at the circumference of the Mohr's circle (Means, 1976).

As an additional aid in interpreting the bone strain data, a metal model of the zygomatic arch region of the skull was constructed. The model consisted of a flat L-shaped piece of steel with one arm of the L representing the horizontal projection of the posterior root of the zygomatic arch and the other arm the cranium. A rosette strain gauge was bonded to the zygomatic arch portion of the model in the same orientation as the *in vivo* gauges had been bonded to the skull. The horizontal projection representing the zygomatic arch was then deformed in pure compression, pure tension, pure torsion and various combinations of these to determine the expected strain in a deformed cantilever beam. Although the model is a gross simplification of the zygomatic arch region of the skull, and the absolute magnitude of strain differed during these manipulations, this technique was useful in comparing the strain recorded in the various elements of the rosette strain gauge during simple deformation of a cantilever beam and the recorded *in vivo* bone strain.

RESULTS

Electromyographic amplitudes during bone biting and mastication

The electromyographic amplitudes recorded during bone biting were higher than those recorded during the mastication of meat. Figure 3 shows a representative record illustrating integrated electromyographic activity during biting on a bone and masticating meat during the same experiment. In order to demonstrate the difference in electromyographic activity levels during mastication and bone-biting in a quantitative manner, integrated electromyographic amplitudes during individual bites were converted to a percentage of the maximum value recorded from that electrode during the experiment. Comparisons of the integrated working-side electromyographic amplitudes as a percentage of the maximum value recorded from two animals in three experiments are shown in Table 1. The mean values of integrated electromyographic activity during bone biting are much higher for both the temporalis and masseter muscles and are statistically significantly different (Mann–Whitney test, 0·05 level).

Patterns between balancing- and working-side muscles

All the animals readily bit on bones while lying in a prone position. They positioned the bone between their carnassial teeth with their forepaws and were able to apply forces large enough to splinter and in some cases crush the bone. A representative example of surface electromyographic activity recorded while a dog was biting on bone at the carnassial teeth is shown in Figure 4. Note that the electromyographic activity from the biting or working-side jaw-elevator muscles exceeds that from the opposite or balancing-side muscles. This was a consistent finding for both the temporalis and masseter muscles during medium and large amplitude electromyographic responses during bone biting.

In order to quantify the differences between balancing- and working-side electromyographic activities, electromyographic outputs were standardised as before. In Figure 5, integrated electromyographic activity as a percentage of the maximum is plotted for individual bites. It can be seen in this Figure, taken from one experiment, that balancing-side electromyographic activity is less than that of the working-side through a wide range of electromyographic amplitudes.

Table 1. *Comparison of integrated electromyographic activity during biting and mastication*

	n	Mean (%)	Range (%)	S.D.
Temporalis integrated electromyographic amplitude during bone biting	72	55	15–100	26
Temporalis integrated electromyographic amplitude during mastication	100	12	2–35	6
Masseter integrated electromyographic amplitude during bone biting	59	53	10–100	23
Masseter integrated electromyographic amplitude during mastication	95	28	7–90	16

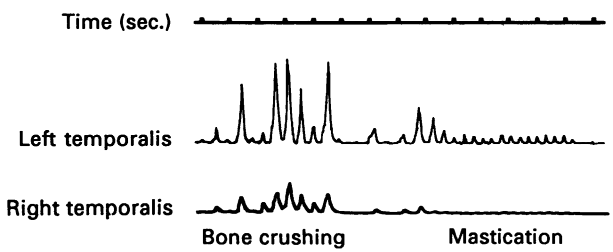

Fig. 3. Integrated surface electromyographic activity during biting on bone and mastication at the left carnassial teeth.

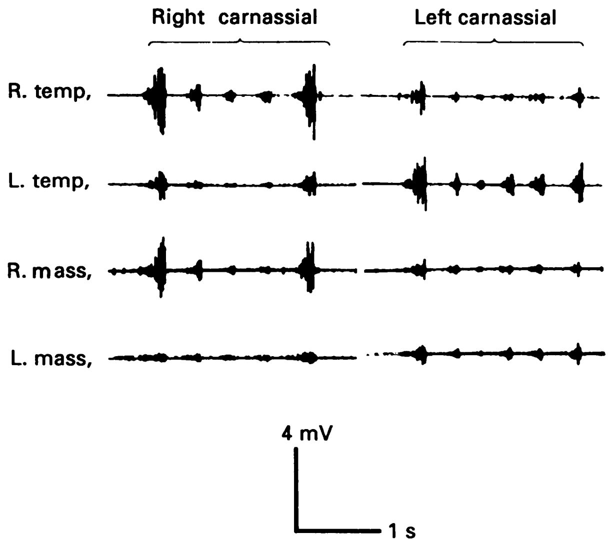

Fig. 4. Representative surface electromyographic activity during isometric biting on bone at the carnassial teeth.

This trend of greater working-side jaw-adductor electromyographic activity than balancing-side activity was consistently seen in different animals and different experiments. Figure 6 shows clearly that the integrated electromyographic activity of the working side exceeds that of the balancing side in spite of the differences in electrode placement and inter-individual variability.

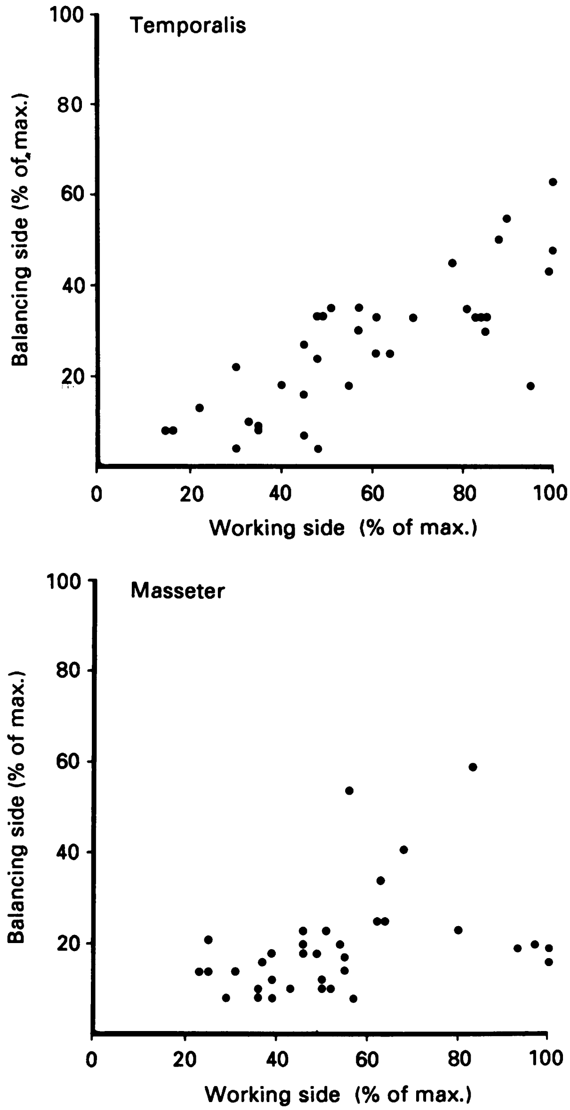

Fig. 5. Integrated surface electromyographic output during isometric biting on bone at the carnassial teeth from one animal during one recording session. Vertical and horizontal axes represent balancing- and working-side electromyographic output plotted as a percentage of the maximum electromyographic value for each electrode. Each point represents one bite.

During mastication, only the temporalis muscle showed greater activity on the working side as shown in Figure 7. The Figure illustrates that balancing-side temporalis electromyographic activity is much less than that of the working side during mastication while masseter muscle electromyographic levels during mastication show no particular pattern.

The recordings from indwelling electromyographic electrodes were used merely to determine if all parts of a particular muscle were active during bone biting and mastication. It was found by visual examination of 80 bone-crushing bites that all portions of the temporalis muscle were active on both the balancing and working sides. Since electromyographic activity was not standardised, specific comparisons

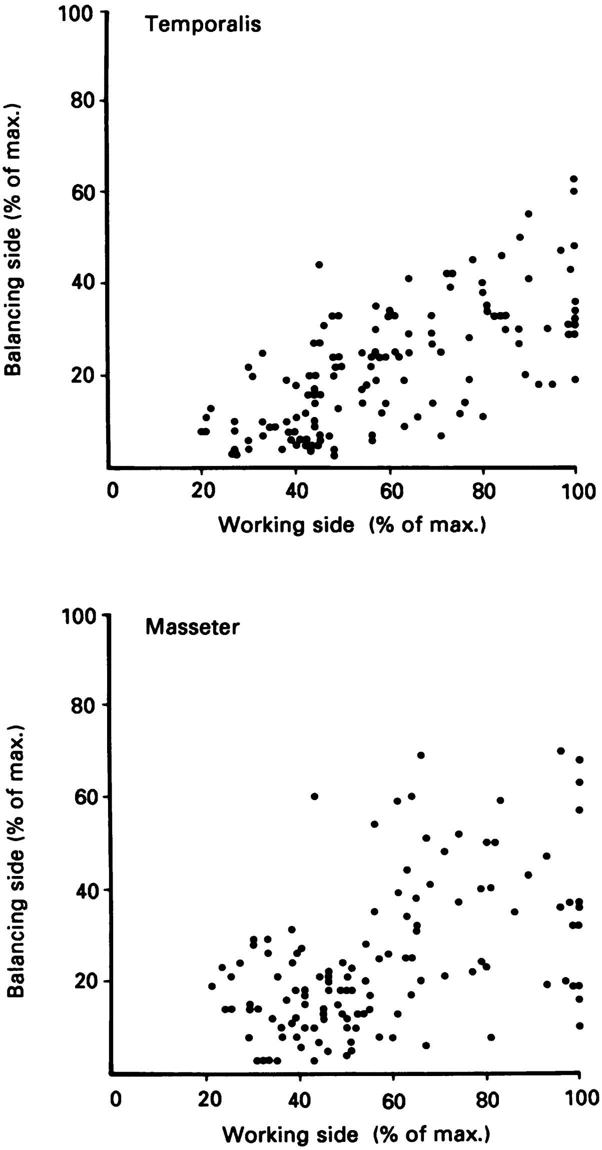

Fig. 6. Combined plot of integrated surface electromyographic output during isometric biting at the carnassial teeth from four animals during four recording sessions. n = 137.

were not possible. Examination of indwelling electromyographic activity from portions of the masseter muscle during 70 bites on bone showed that both the deep and superficial portions of the muscle were active in all cases.

Analysis of indwelling electromyographic activity during the mastication of meat showed a much less constant pattern of activity. Temporalis electromyographic activity during mastication was examined visually in 63 cases and showed extremely reduced electromyographic activity from the posterior portion of the balancing-side temporalis muscle. Although it appeared that all portions of the masseter muscle were active during some phase of jaw closure in the 96 sequences examined, different parts of the muscle appeared to be active during different phases. Since no accurate record

Fig. 7. Combined plot of the integrated surface electromyographic activity during the mastication of meat. The points are from two animals during three recording sessions. n = 78.

of jaw movement was recorded in these experiments, it was not possible to determine these relationships more precisely.

Indwelling electromyographic activity from the medial pterygoid muscle demonstrated that it was active during both bone biting and mastication and that electromyographic amplitudes were generally greater during bone biting than during mastication.

Bone strain produced during muscle simulation

The manipulation of ligamentous preparations showed that the application of simulated muscle activity with a well-developed occlusal fulcrum resulted in a repeatable direction of condylar movement which was independent of the magnitude of the applied force. When a clear occlusal fulcrum such as a bone exists at the carnassial teeth, simulated working-side muscle forces could produce either tensile or compressive forces at the working-side jaw joint. In contrast to this, simulated balancing-side muscle forces produced only tension at the site of the strain gauge on the working side.

Pushing the mandibular condyle dorsally to simulate a compressive force on the condyle resulted in a compressive strain output from the strain gauge on the dorsal surface of the zygomatic arch (Fig. 8*a*). Pulling the mandibular condyle ventrally to simulate tensile loading of the joint resulted in a tensile strain output from the strain gauge (Fig. 8*b*). When a simulated temporalis muscle force was applied to the working side of the mandible, a compressive or tensile joint force was produced depending upon the precise line of action simulated. If the line of muscle action passed anterior to (i.e. above) the carnassial bite point, a tensile strain on the zygomatic arch was recorded (Fig. 8*c*). This type of strain is proposed to have been produced by a ventral movement of the ipsilateral mandibular condyle. Conversely, if the line of action of the simulated muscle force was directed caudal to the bite point, a compressive bone strain was recorded (Fig. 8*d*). This strain is similar to that produced during compressive manipulation of the mandibular condyle and was probably produced by a dorsal movement of the ipsilateral condyle bending the zygomatic arch dorsally.

When a simulated masseter muscle force was applied to the working side of the mandible with a carnassial bite point, only a compressive strain could be produced on the dorsal surface of the zygomatic arch. This strain was presumably the result of the mandibular condyle bending the zygomatic arch dorsally (Fig. 8*e*).

If the simulated temporalis or masseter muscle force was applied contralateral to the bite point, the recorded bone strain on the dorsal surface of the zygomatic arch was invariably tensile (Fig. 8*f*, *g*). This bone strain was correlated with movement of the mandibular condyle ventrally and anteriorly through the ligamentous portion of the joint capsule. Repeated simulations of the balancing-side temporalis or masseter muscle force stressed the anterior portion of the working-side joint capsule so much that it eventually ruptured the joint capsule and dislocated the jaw joint.

Bone strain produced during muscle stimulation

Manipulations of the mandibular condyle during the jaw-muscle stimulation experiments produced the bone strains shown in Table 2. Pushing the mandible dorsally produced a combination of compressive and tensile bone strain. The minimum principal strain ($\epsilon 2$) was negative (i.e. compressive) and of a larger absolute value than the maximum principal strain ($\epsilon 1$). This combination of strains is indicative of a torsional and compressive stress. Pulling the mandible ventrally also produced compressive and tensile bone strain at the strain gauge site. In this situation the minimum principal strain was negative (i.e. compressive) but the maximum principal strain ($\epsilon 1$) was positive (i.e. tensile) and of a larger absolute value, implying a torsional and tensile stress.

Stimulation of the right temporalis muscle produced a combination of compressive and tensile bone strain on the dorsal surface of the left (working-side) zygomatic arch underlying the strain gauge (Table 3). Since the maximum principal strain is positive (i.e. tensile) and larger than the absolute value of the negative (i.e. compressive) minimum principal strain, these data are indicative of a torsional and tensile stressing of the bone.

Stimulation of the left temporalis or masseter muscles produced a combination of tensile and compressive bone strain on the dorsal surface of the left zygomatic arch in all but one instance (Tables 4, 5). The minimum principal strain ($\epsilon 2$) was negative (i.e.

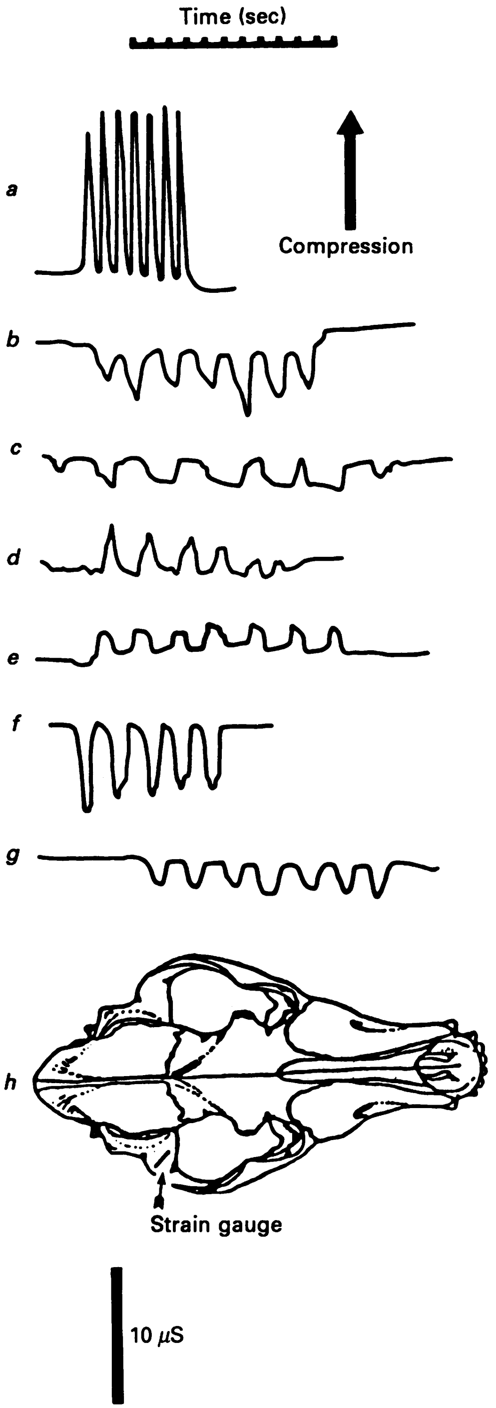
Time (sec)
Compression
a
b
c
d
e
f
g
h
Strain gauge
10 μS

Table 2. *Bone strain recorded from the left zygomatic arch of Dog 3057 while manipulating the left jaw joint*

		Principal strains						Angle of maximum principal strain[a]		
		Maximum (ϵ1)			Minimum (ϵ2)					
Manipulation	n	Mean (μS)	Largest (μS)	S.D.[b]	Mean (μS)	Largest (μS)	S.D.[b]	Mean (deg.)	Range (deg.)	S.D.[b]
Pushing the condyle dorsally	10	56	68	11	−97	−102	8	44	−86 to 89	18[c]
Pulling the condyle ventrally	16	96	114	18	−64	−77	15	75	74 to 76	0.8

[a] Relative to strain gauge no. 1.
[b] S.D., standard deviation.
[c] Since the range of the angle of maximum principal strain contained both positive and negative values, the calculated standard deviation is large despite an actual range of only 5 degrees.

Table 3. *Bone strain recorded from the left zygomatic arch of Dog 3057 while stimulating the right temporalis muscle*

		Principal strains						Angle of maximum principal strain[a]		
		Maximum (ϵ1)			Minimum (ϵ2)					
Bite point	n	Mean (μS)	Largest (μS)	S.D.	Mean (μS)	Largest (μS)	S.D.	Mean (deg.)	Range (deg.)	S.D.
Left canine	5	56	61	3	−24	−25	2	8	4 to 12	4
Left carnassial	4	159	159	0	−66	−66	0	44	44	0

[a] Relative to strain gauge no. 1.

compressive) in all cases and exceeded that of the maximum principal strain. This combination indicates a torsional and compressive stress applied to the region where bone strain was recorded. The one instance which was different was during stimulation of the left temporalis muscle with the bite point positioned at the left carnassial teeth. During this stimulation both the maximum and minimum principal strains were negative (i.e. compressive) and therefore indicate a general compressive stress.

Stimulation of both temporalis and masseter muscles produced combinations of compressive and tensile bone strain with the bite point positioned at the right canine or carnassial teeth or the left canine teeth (Table 6). This combination of strains is indicative of a torsional and compressive stress since the minimum principal strain (ϵ2)

Fig. 8(*a–h*). Representative results of the manipulation of a ligamentous preparation with a strain gauge bonded to the dorsal surface of the right zygomatic arch. (*a*) Compressive bone strain resulting from pushing the right mandibular condyle dorsally. (*b*) Tensile bone strain resulting from pulling the right mandibular condyle ventrally. (*c*) Tensile bone strain produced by simulation of the posterior portion of the right temporalis muscle with a bite point positioned at the right carnassial teeth. (*d*) Compressive bone strain produced by simulation of the anterior portion of the right temporalis muscle. (*e*) Compressive bone strain produced by simulation of the right masseter muscle with the bite point positioned at the right carnassial teeth. (*f*) Tensile bone strain produced by simulation of the left temporalis muscle with the bite point positioned at the right carnassial teeth. (*g*) Tensile bone strain produced by simulation of the left masseter muscle with the bite point positioned at the right carnassial teeth. (*h*) Dorsal view of the ligamentous preparation showing the location of the single element strain gauge.

Table 4. *Bone strain recorded from the left zygomatic arch of Dog 3057 while stimulating the left temporalis muscle*

		Principal strains						Angle of maximum principal strain[a]		
		Maximum ($\epsilon 1$)			Minimum ($\epsilon 2$)					
Bite point	n	Mean (μS)	Largest (μS)	S.D.	Mean (μS)	Largest (μS)	S.D.	Mean (deg.)	Range (deg.)	S.D.
Left canine	4	18	22	3	−109	−112	4	−81	−77 to 85	3
Right carnassial	4	37	40	3	−83	−88	4	69	68 to 71	2
Left carnassial	4	−7	−9	2	−40	−44	3	−19	−17 to 23	3

[a] Relative to strain gauge no. 1.

Table 5. *Bone strain recorded from the left zygomatic arch of Dog 3057 while stimulating the left masseter muscle*

		Principal strains						Angle of maximum principal strain[a]		
		Maximum ($\epsilon 1$)			Minimum ($\epsilon 2$)					
Bite point	n	Mean (μS)	Largest (μS)	S.D.	Mean (μS)	Largest (μS)	S.D.	Mean (deg.)	Range (deg.)	S.D.
Left canine	5	199	209	55	−322	−327	4	75	74 to 76	0·8
Right carnassial	5	213	222	7	−228	−243	10	83	83 to 85	0·8
Left carnassial	5	156	163	7	−172	−187	17	75	74 to 76	1

[a] Relative to strain gauge no. 1.

Table 6. *Bone strain recorded from the left zygomatic arch of Dog 3057 while stimulating both temporalis and both masseter muscles*

		Principal strains						Angle of maximum principal strain[a]		
		Maximum ($\epsilon 1$)			Minimum ($\epsilon 2$)					
Bite point	n	Mean (μS)	Largest (μS)	S.D.	Mean (μS)	Largest (μS)	S.D.	Mean (deg.)	Range (deg.)	S.D.
Right canine	5	57	64	6	−132	−148	10	77	77 to 78	0·6
Left canine	5	41	50	7	−64	−92	18	79	78 to 80	1
Right carnassial	5	77	83	7	−179	−198	18	76	74 to 77	1
Left carnassial	5	53	53	0·3	10	15	4	−16	88 to 87	94

[a] Relative to strain gauge no. 1.

was negative (i.e. compressive) and its absolute value exceeded that of the maximum principal strain. When the bite block was positioned at the left carnassial teeth while stimulating the temporalis and masseter muscles, only tensile strain was recorded from the left (working-side) zygomatic arch. Since the maximum principal strain and the minimum principal strain were both positive (i.e. tensile), a general tensile stress is indicated.

The results of bone strain produced by muscle stimulations in dog 1296 are shown in Table 7. During stimulation of the left temporalis muscle with the bite block positioned at the left carnassial teeth only negative (i.e. compressive) bone strain was recorded, indicating a general compressive stress. When the left masseter or right

Table 7. *Bone strain recorded from the left zygomatic arch of Dog 1296 with the bite point at the left carnassial teeth*

		Principal strains								
		Maximum (ϵ1)			Minimum (ϵ2)			Angle of maximum principal strain[a]		
Muscle stimulated	n	Mean (μS)	Largest (μS)	S.D.	Mean (μS)	Largest (μS)	S.D.	Mean (deg.)	Range (deg.)	S.D.
Left temporalis	20	−19	−29	36	−71	−129	5	−19	−7 to 28	5
Left masseter	18	9	21	24	−37	−74	24	46	39 to 54	6
Right temporalis	20	4	5	0·3	−12	−15	2	38	38 to 41	2
Right masseter	13	7	14	3	0·5	−6	3	40	81 to 91	54

[a] Relative to strain gauge no. 1.

temporalis muscle was stimulated with the bite block positioned at the left carnassial teeth both negative (i.e. compressive) and positive (i.e. tensile) strains were recorded. The value of the minimum principal strain was negative (i.e. compressive) and of greater absolute value than that of the maximum principal strain indicating a combination of torsional and compressive stress. When the right (balancing-side) masseter muscle was stimulated, both the maximum and minimum principal strains were small and positive (i.e. tensile) indicating a general tensile stress on the left (working-side) zygomatic arch.

Interpretation of jaw-joint loading from bone strain

The extrapolation of jaw-joint loading from bone strain recorded during the muscle simulations was based upon correlations with bone strain recorded during manipulations of the mandibular condyle.

Correlations between bone strain and jaw-joint manipulations showed that working-side jaw-elevator muscle stimulation produced compressive bone strain similar to that recorded during pushing the mandibular condyle dorsally. The one exception to this was that when the line of action of the simulated temporalis muscle force was anterior to the carnassial bite point, a tensile bone strain was recorded. Tensile loading of the jaw joint is predicted when the line of action of the elevator muscle is anterior to the bite point (Bramble, 1978). This situation seems unlikely to exist *in vivo*, however, because it requires the selective recruitment of only a few of the most posteriorly directed temporalis muscle fibres which was not seen during electromyographic recording.

Simulation of balancing-side muscle activity with a bite point at the carnassial teeth produced a tensile bone strain similar to that recorded when the mandibular condyle was pulled ventrally. Since the surrounding tissues had been removed from these preparations, it was possible to observe the mandibular condyle being forced ventrally and anteriorly against the portion of the joint capsule during these simulations. In this instance, therefore, it was possible to confirm visually the correlation between bone strain and jaw-joint loading.

The anterior component of this condylar movement appeared to be caused by the mandibular condyle sliding down the post-glenoid process. Purely ventral movements of the condyle would then be converted into ventrally and anteriorly directed movement (Fig. 9). To test this interpretation, manipulations were carried out in another ligamentous preparation before and after removal of the hook of the post-glenoid process. After removal of the distal portion of the post-glenoid process,

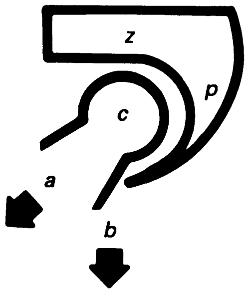

Fig. 9. Schematic cross-section of the medial portion of the canid jaw-joint region showing the type of condylar movement observed during balancing-side muscle simulation with a bite-point at the ipsilateral carnassial teeth. *a*, anteroventral movement of the mandibular condyle seen during the balancing-side muscle simulations and produced by the mandibular condyle sliding down the inner surface of the post-glenoid process. *b*, pure ventral movement of the mandibular condyle seen during balancing-side muscle simulations after removal of the post-glenoid process. *c*, mandibular condyle; *p*, post-glenoid process; *z*, zygomatic arch. Anterior is to the left of the page, dorsal towards the top of the page.

balancing-side muscle simulation with the bite point positioned at the carnassial teeth resulted in purely ventral movement of the working-side mandibular condyle, thus confirming the original interpretation.

The extrapolation of jaw-joint loading from bone strain recorded during stimulation of the jaw muscles was based upon comparisons with bone strain during manipulation of the mandibular condyle and during deformation of the model of the zygomatic arch.

Stimulation of individual jaw-adductor muscles with the bite point at either canine or carnassial teeth resulted in two basic patterns of bone strain on the zygomatic arch: (1) combined compression and torsion and (2) tension (Tables 3–7). Compression and torsion of the zygomatic arch resulted from all except two combinations of muscle stimulation and bite-point location; this pattern was similar to that produced by pushing the mandibular condyle dorsally (Tables 2–7). A representative Mohr's circle for these data is shown in Figure 10*a*; it resembles that recorded during a dorsal bending and clockwise torsion of the zygomatic arch model. This bone strain is interpreted as resulting from the mandibular condyle pushing dorsally and slightly anteriorly against the zygomatic arch as shown diagrammatically to the right in Figure 10*a*.

The combinations of muscle stimulation and bite-point location which did not produce compressive joint loading were stimulation of either the balancing-side temporalis or masseter muscles with the bite block positioned at the working-side carnassial teeth. During stimulation of the balancing-side temporalis muscle in Dog 3057, the maximum principal strain was positive (i.e. tensile) and exceeded that of the minimum principal strain (Table 3). A Mohr's circle from the averaged strain data is shown in Figure 10*b* and is similar to that recorded during a pure ventral bending of the zygomatic arch model (Fig. 10*e*). This bone strain pattern is therefore interpreted as resulting from a ventral movement of the mandibular condyle as shown diagrammatically to the right of Figure 10*b*. Stimulation of the balancing-side temporalis muscle in Dog 1296 produced a very small strain on the working-side zygomatic arch which was slightly compressive since the minimum principal strain was negative and its absolute value exceeded that of the maximum principal strain. During stimulation of the balancing-side masseter muscle in Dog 1296, both the minimum and maximum principal strains recorded were small and positive (i.e. tensile). A

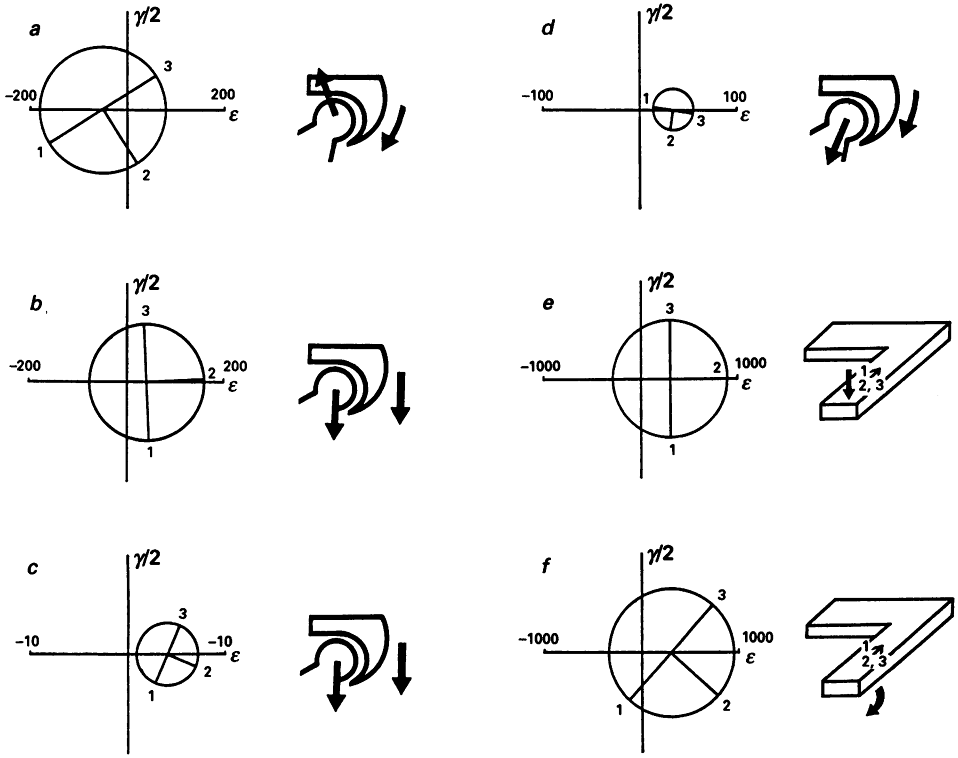

Fig. 10(*a–f*). Types of strain recorded on the dorsal surface of the left zygomatic arch during various muscle stimulations (strain gauge orientation is shown in Fig. 2). The horizontal axis (ϵ) indicates the principal strain while the vertical axis ($\gamma/2$) indicates the shear strain. Tensile strain occurs in the positive portion of the (ϵ) axis, clockwise torsional strain occurs in the positive portion of the ($\gamma/2$) axis. The numbers 1, 2 and 3 on the Mohr's circle represent the orientation of the individual elements of the rosette strain gauge. (*a*) Mohr's circle showing representative strains recorded during stimulation of the left (working-side) masseter muscle with a bite point located at the left carnassial teeth, or stimulation of the right or left masseter muscle with the bite point positioned at the right or left canine teeth, or simultaneous stimulation of the right or left masseter muscles and the right and left temporalis muscles with the bite point at either the left or right canine or the right carnassial teeth. To the right of Mohr's circles (*a–d*) is a diagrammatic parasagittal section through the jaw joint region showing the proposed direction of movement of the mandibular condyle and deformation of the zygomatic arch during each stimulation. (*b*) Mohr's circle from the averaged strain recorded in Dog 3057 during stimulation of the right (balancing-side) temporalis muscle with the bite point located at the left carnassial teeth. (*c*) Mohr's circle from the averaged strain recorded in Dog 1296 during stimulation of the right (balancing-side) masseter muscle with the bite point located at the left carnassial teeth. (*d*) Mohr's circle from the averaged strain recorded during simultaneous stimulation of the right and left temporalis and right and left masseter muscles with the bite point located at the left carnassial teeth. (*e*) Mohr's circle showing the type of strains recorded during ventral bending of a model of the zygomatic arch. To the right of the Mohr's circles (*e*) and (*f*) is a diagram of the zygomatic arch model with a strain gauge bonded to the portion representing the horizontal projection of the zygomatic arch. The strain gauge is therefore in approximately the same orientation as the strain gauge implanted during the muscle stimulations. Anterior is to the left of the page, dorsal is towards the top of the page. (*f*) Mohr's circle showing the type of strains recorded during ventral bending and counter-clockwise torsion of the zygomatic arch model.

Mohr's circle for the average strain data during these stimulations is shown in Figure 10*c* and is similar to that recorded during a ventral bending and clockwise rotation of the zygomatic arch model as shown in Figure 10*f*. These bone strain data are therefore interpreted as indicative of a ventral bending and slight clockwise rotation of the zygomatic arch caused by a ventral movement of the mandibular condyle. The difference between these two Mohr's circles is that in Figure 10*c* both the minimum and maximum principal strains are positive while in Figure 10*f* the maximum principal strain is negative. The occurrence of only tensile strain as seen in 10*c* could result from the rotational axis for the clockwise torsion being anterior to the strain gauge or the tensile strain produced by ventral bending of the zygomatic arch exceeding the torsional strain. Since both bone-strain interpretations would result from anteroventral movement of the mandibular condyle and produce a deleterious jaw-joint loading, it is not essential for the arguments made here to differentiate between the two. These muscle stimulation experiments therefore corroborate the hypothesis that when a bite point is positioned at the carnassial teeth, balancing-side masseter and temporalis activity produce a ventral movement of the working-side mandibular condyle.

To determine the consequences of bilateral contraction of the jaw-adductor muscles, the masseter and temporalis muscles were stimulated simultaneously. Although it was not possible to verify precisely equal contractions in the right and left side muscles, differences were minimised by stimulating the muscles as strongly as possible. Stimulations with the bite point at either pair of canine teeth or the carnassial teeth on the side opposite the strain gauge were consistent with strains expected from a dorsal bending and torsion of the zygomatic arch (Table 6; Fig. 10*a*). Stimulation of all the muscles with a bite point at the carnassial teeth on the same side as the strain gauge (an indication of the working-side jaw-joint loading) produced a positive (i.e. tensile) minimum and maximum principal strain. The Mohr's circle for the average strain recorded during these stimulations is shown in Figure 10*d* and is most comparable to Figure 10*f* in which the zygomatic arch model was ventrally bent and rotated clockwise. In the stimulation, however, both the minimum and maximum principal strains are positive, indicating a general tension, and can be interpreted as the axis of rotation being anterior to the strain gauge or the tensional stress exceeding the torsional stress. Here again, both interpretations are consistent with an anteroventrally directed condylar movement and a potentially hazardous jaw-joint configuration.

DISCUSSION

Masseter and temporalis electromyographic amplitudes were much higher during bone crushing than mastication and since a positive relationship has been demonstrated between electromyographic activity and bite force (Ahlgren & Owall, 1970; Hagberg, Agerberg & Hagberg, 1985; Hylander & Johnson, 1985; Pruim, Ten Bosch & De Jongh, 1978), it is assumed that much greater bite force is produced during bone crushing. This is very apparent if one considers that pieces of beef shank up to 5 cm in diameter were readily fractured and that indirect measurements of bite forces during these activities are reported to reach 165 kg/10 mm^2 (Triska, 1924). In spite of the large bite forces that were produced, balancing-side muscle activity was never maximally recruited even during the largest electromyographic amplitudes. This is a very surprising finding and, if one assumes that this activity represents nearly maximum production of bite force, as seems likely, is contrary to assumptions made about the recruitment ratio of balancing and working-side muscle activities in carnivores by Greaves (1983). A possible explanation for the observed recruitment pattern, which follows from various geometrical models of jaw-muscle and jaw-joint interactions (Smith, 1978; Greaves, 1983; Weijs, 1981), is that jaw-adductor muscle activity is constrained by the need to maintain mechanical stability of the jaw joint.

The mechanical models of the jaw proposed by Smith (1978) for primates, Weijs (1981) for humans, and Greaves (1983) for carnivores all predict the ventral movement

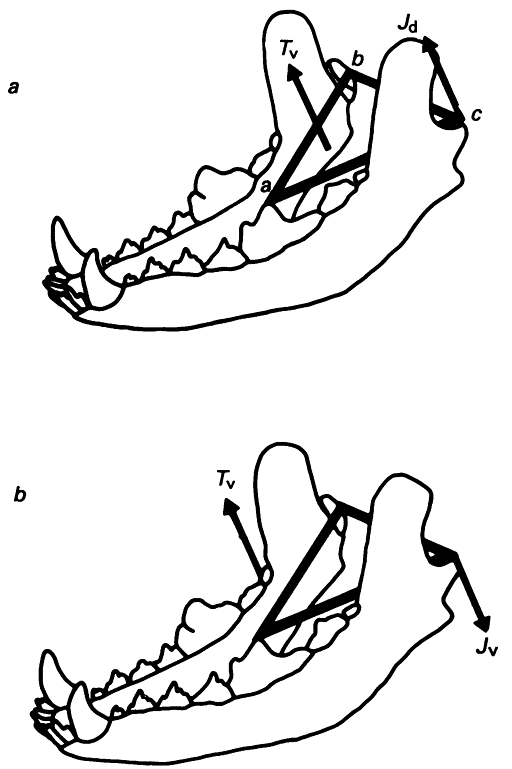

Fig. 11 (*a–b*). (*a*) Representation of the lower jaw with the vertical adductor muscle vector (T_v) within the triangle of support therefore producing a dorsal movement of the working-side mandibular condyle (J_d) and compressive bone strain on the zygomatic arch. (*b*) Representation of the lower jaw with the vertical component of the adductor muscle force (T_v) positioned outside the triangle of support as it would be during simulation and stimulation of the balancing-side muscles alone. This configuration would produce a ventral movement of the working-side mandibular condyle (J_v). *a*, The bite point at the carnassial tooth; *b*, the balancing-side mandibular condyle; *c*, the working-side mandibular condyle. Together *a*, *b* and *c* comprise the triangle of support proposed by Greaves (1983).

of the working-side mandibular condyle reported here during balancing-side muscle simulation and stimulation. In the model proposed by Greaves, jaw-adductor muscle activity is reduced to a single vertical muscle resultant whose location depends upon the anteroposterior location of the jaw muscles and the ratio of balancing- to working-side muscle activity. If the total vertical muscle resultant falls within the 'triangle of support' region bounded by the two mandibular condyles and the bite point, loading at both jaw joints will be compressive (Fig. 11 *a*). If only balancing-side muscle activity is activated, the total vertical muscle resultant will fall outside the 'triangle of support' and rotate the mandible clockwise around an axis through the carnassial bite point and the balancing-side mandibular condyle (Fig. 11 *b*) and thus move the working-side mandibular condyle ventrally.

The results of the muscle simulations described here are consistent with the theoretical predictions of these geometrical models. The simulations showed that working-side jaw muscle activity produced compressive bone strain and a compressive jaw-joint loading. More importantly for the hypothesis being considered here, balancing-side muscle simulation produced consistent anteroventral movement of the working-side mandibular condyle which eventually ruptured the joint capsule.

Stimulating the jaw-adductor muscles with a well-defined occlusal fulcrum produced bone strain on the zygomatic arch which was also consistent with both the theoretical predictions of jaw-joint loading. Working-side muscle activity by itself produced a bone strain consistent with a compressive loading of the working-side mandibular condyle, while balancing-side masseter or temporalis muscle activity alone produced a bone strain indicative of a ventral movement of the working-side mandibular condyle. Approximately equal stimulations of both the balancing- and working-side adductor muscles, with a carnassial bite point, produced bone strain indicative of a ventral movement of the working-side mandibular condyle. This suggests that equal recruitment of the working- and balancing-side adductor muscles, with a carnassial bite point, produces a mechanically precarious jaw-joint loading in which the mandibular condyle is moved slightly anteroventrally. Since the dog possesses only a very reduced preglenoid process, this type of condylar movement could be resisted only by the soft tissues of the anterior portion of the joint capsule and would predispose the joint to dislocation. Dislocation of the jaw joint in dogs has only rarely been reported (Lane, 1982; Robins & Grandage, 1977; Stewart, Baker & Lee, 1975), therefore this type of joint loading cannot be common. If a greater percentage of working-side muscle activity is recruited, the total vertical muscle resultant (T_v in Figure 11) is moved towards the working side and produces dorsally directed condylar movements against the bony zygomatic arch (see also Weijs, 1980).

Not only was the amount of muscle activity during mastication much less than that during isometric biting, but the pattern of activity between the balancing- and working-side muscle was also clearly different. The balancing-side temporalis muscle was only slightly activated during mastication while the balancing-side masseter muscle was approximately as active as that of the working side. Since a rigid occlusal fulcrum would not have been present when masticating meat, it is hypothesised that balancing-side muscle activity during mastication does not produce ventral condylar movement. Differences in jaw-adductor muscle activity during mastication therefore may be related to alignment of the carnassial teeth as suggested by Scapino (1965).

This study has shown that balancing-side muscles are not maximally recruited during mastication and bone crushing and therefore large bite forces in the domestic dog are not produced by maximal jaw-adductor muscle contraction. It is proposed therefore that the maintenance of jaw-joint stability supersedes the production of bite force.

SUMMARY

Electromyographic activity from the jaw-adductor muscles was recorded during mastication and bone crushing in domestic dogs (*Canis familiaris*). During mastication, balancing-side temporalis electromyographic activity was much less than that of the working side while masseter muscle electromyographic activities were of similar amplitude. Despite the large bite forces that were produced during bone crushing, balancing-side masseter and temporalis electromyographic activities were always smaller than the working-side electromyographic amplitudes. Based upon geometric modelling, it is proposed that balancing-side muscle activity is reduced because of its tendency to produce mechanically disadvantageous jaw-joint forces. This hypothesis was tested by correlating bone strain adjacent to the jaw joint measured during manipulations of the mandibular condyle with bone strain recorded during the simulation and stimulation of jaw-adductor muscle activity. Working-side muscle activity produced bone strain that correlated with a compressive joint loading, while balancing-side muscle activity, with an occlusal fulcrum at the carnassial teeth,

produced bone strain indicative of an anteroventral movement of the working-side mandibular condyle which eventually ruptured the joint capsule. When the temporalis and masseter muscles were stimulated bilaterally with a carnassial bite point, bone strain indicative of a ventrally directed and potentially damaging condylar movement was produced. It is proposed that working-side muscle activity exceeds balancing-side muscle activity during carnassial biting to maintain jaw-joint stability.

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