LETTER

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Impact of meat and Lower Palaeolithic food processing techniques on chewing in humans

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The origins of the genus *Homo* are murky, but by *H. erectus*, bigger brains and bodies had evolved that, along with larger foraging ranges, would have increased the daily energetic requirements of hominins[1,2]. Yet *H. erectus* differs from earlier hominins in having relatively smaller teeth, reduced chewing muscles, weaker maximum bite force capabilities, and a relatively smaller gut[3–5]. This paradoxical combination of increased energy demands along with decreased masticatory and digestive capacities is hypothesized to have been made possible by adding meat to the diet[6–8], by mechanically processing food using stone tools[7,9,10], or by cooking[11,12]. Cooking, however, was apparently uncommon until 500,000 years ago[13,14], and the effects of carnivory and Palaeolithic processing techniques on mastication are unknown. Here we report experiments that tested how Lower Palaeolithic processing technologies affect chewing force production and efficacy in humans consuming meat and underground storage organs (USOs). We find that if meat comprised one-third of the diet, the number of chewing cycles per year would have declined by nearly 2 million (a 13% reduction) and total masticatory force required would have declined by 15%. Furthermore, by simply slicing meat and pounding USOs, hominins would have improved their ability to chew meat into smaller particles by 41%, reduced the number of chews per year by another 5%, and decreased masticatory force requirements by an additional 12%. Although cooking has important benefits, it appears that selection for smaller masticatory features in *Homo* would have been initially made possible by the combination of using stone tools and eating meat.

Two derived human behaviours are meat eating and food processing. Archaeological and palaeontological evidence indicate that hominins began to increase meat consumption by at least 2.6 million years ago (Ma) (ref. 7), and until the invention of agriculture, meat was an indispensable component of human diets[15]. Archaeological data also indicate that hominins fabricated stone tools by 3.3 Ma (ref. 10), learned to control fire by 1 Ma (ref. 13), and started to cook on a regular basis by at least 0.5 Ma (refs 13, 14). Today, humans process most of their food in some way before ingestion. Yet, despite the importance of meat eating and food processing, little is currently known about the degree to which these novel behaviours altered selection on the hominin masticatory apparatus. Multiple lines of evidence indicate that the australopith ancestors of *Homo* consumed lots of mechanically demanding plant foods[16] and probably resembled great apes in spending a substantial proportion of the day feeding and chewing, approximately an order of magnitude more than non-industrial humans[17]. Maximum bite force capabilities in early *Homo* were less than half that of australopiths[3], and while *H. habilis* retained many primitive masticatory features, including large, thick post-canine teeth, *H. erectus* had considerably smaller post-canines, along with smaller faces. These derived masticatory features suggest that the genus *Homo* consumed foods that were easier to eat, requiring fewer, less forceful chews and reducing the need for high maximum bite forces. But it has been unclear to what extent these shifts were made possible by meat, by mechanical processing, or by cooking.

Efforts to understand how diets differed between australopiths and early *Homo* have focused on increased consumption of meat (muscle tissue) and the benefits of cooking[6,12,18]. Muscle tissue is calorically denser than most plant foods, but is difficult to chew with low-crested (bunodont) hominoid molars. Chimpanzees reportedly spend approximately 5–11 h chewing small (~4 kg) animals[19], and although the carcasses include hide, cartilage and other tough tissues, such lengthy times highlight the challenges of masticating unprocessed meat using low-crested teeth. Consequently, apart from not knowing how much meat early hominins ate, it remains unclear how much adding unprocessed meat to the diet would have affected their ability to chew, especially before cooking became common. Simple cooking methods such as roasting make it easier to chew meat by stiffening muscle fibres and reducing energy dissipation during fracture[20]. Cooking also tends to make plant tissue softer and tenderer, because heat degrades polysaccharides such as pectin and weakens intercellular bonds[20–22]. Another benefit of cooking is to increase the overall energetic yield of both meat and plants[23,24].

It is also important to consider mechanical processing, which is a simpler and older technology. Early *Homo* probably used Lower Palaeolithic tools in at least three ways to process food mechanically. First, rocks can be used to tenderize foods by pounding and grinding, the former of which is observed among chimpanzees[25]. Second, stone flakes are effective for slicing foods into smaller pieces that require fewer chews to consume. Finally, flakes or choppers can be used to remove skin, cartilage, rinds, and other mechanically demanding tissues that are challenging to chew. An added benefit of mechanical processing techniques is to increase net energy yield by breaking down tissues and cell walls, making nutrients more directly accessible to digestion and increasing the surface area to volume ratios of ingested particles[23,24].

Given evidence for meat consumption and the ability to make simple stone tools long before cooking became common, it has long been hypothesized that increased carnivory and the use of Lower Palaeolithic technology made possible selection for smaller teeth and maximum bite forces, as well as other changes in masticatory anatomy evident in *Homo*[6–10]. However, to test these hypotheses it is necessary to compare how mechanical food processing and cooking affect two key masticatory parameters for both meat and plant foods: the muscular effort required for chewing, and how well the food is fragmented (comminuted) before it is swallowed. We therefore measured chewing performance in adult human subjects fed size-standardized samples of meat, as well as USOs, which are hypothesized to have been a particularly important component of the hominin diet[26]. For meat, we used goat, which is relatively tough and therefore more similar to wild game than domesticated beef; for USOs, we used jewel yams, carrots and beets. As described in Methods, these samples were either unprocessed, processed using the two simplest mechanical processing methods available to Lower

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Table 1 | Average number of chews and masticatory force used per kcal of USOs and meat

Food		Chews per sample	Applied force per sample (N.s)*	Sample weight (g)	Caloric content (kcal g^{-1}) †	Chews per kcal‡	Applied force per kcal (N.s)‡
USOs§ ($n = 14$)	Unprocessed	25.2 (±9.2)	1,105.1 (±539.7)	2.2	0.57	20.1 (± 7.4)	881.3 (±430.4)
	Sliced	26.3 (±10.2)	1,149.3 (±608.6)	2.2	0.57	20.9 (±8.2)	916.5 (±485.3)
	Pounded	24.2 (±10.0)	973.2 (±545.5)	2.1	0.57	20.2 (±8.4)	813.0 (±455.8)
	Roasted	22.4 (±8.9)	870.6 (±489.6)	2.6	0.56	15.4 (±6.1)	597.9 (±336.3)
Meat ($n = 10$)‖	Unprocessed	40.1 (±19.1)	1,546.6 (±927.8)	3.0	1.09	12.3 (±5.8)	473.0 (±283.7)
	Sliced	31.2 (±22.0)	1,099.1 (±1,025.5)	3.0	1.09	9.6 (±6.7)	336.1 (±313.6)
	Pounded	42.1 (±21.7)	2,033.8 (±1,643.0)	3.0	1.09	12.9 (±6.6)	622.0 (±502.4)
	Roasted	45.3 (±24.8)	1,924.2 (±850.2)	3.0	1.43	10.6 (±5.8)	448.5 (±198.2)

Data in brackets are ± 1 s.d.
*Applied masticatory forces were calculated using subject-specific calibration equations that estimate the force–time integral (in N.s) at the M1 from balancing masseter electromyography (EMG) voltage (see Methods).
†Food caloric density was obtained from the US Department of Agriculture (USDA) National Nutrient Database for Standard Reference (http://www.ars.usda.gov/ba/bhnrc/ndl). Sliced and pounded foods were assumed to have the same caloric content as unprocessed foods. Roasted USO data were unavailable, and baked or boiled data were used instead. Unprocessed/sliced/pounded foods: jewel yam = 0.86 kcal g^{-1}; red beetroot = 0.43 kcal g^{-1}; carrot = 0.41 kcal g^{-1}; goat meat = 1.09 kcal g^{-1}. Roasted foods: jewel yam = 0.90 kcal g^{-1}; red beetroot = 0.44 kcal g^{-1}; carrot = 0.35 kcal g^{-1}; goat = 1.43 kcal g^{-1}.
‡Number of chews and applied masticatory force per kcal of food was calculated by dividing chew number or force per sample by average sample weight and then average caloric density.
§Yam, carrot and beetroot data averaged.
‖Masseter muscle activity was not quantified for one subject, reducing sample size to nine for force per kcal.

Palaeolithic hominins (slicing and pounding), or processed by roasting, the simplest form of cooking.

Comparisons of the number of chews and total applied force required to chew different foods until they were ready to be swallowed (Table 1) indicate that considerably less masticatory effort is required to consume unprocessed meat than USOs. Compared to unprocessed USOs, one kcal of unprocessed meat required on average 39% fewer chews and 46% less force to prepare for swallowing ($P = 0.01$ and $P = 0.02$, respectively). However, the participants we studied were unable to reduce effectively the particle sizes of unprocessed meat through mastication. As Fig. 1 illustrates, even after 40 chews, meat boli were predominately comprised of one large particle (Extended Data Table 1). Therefore, although unprocessed meat requires fewer chews and less force per calorie than USOs, the inability of hominin teeth to break raw, unprocessed meat into small particles probably reduced net energy gain from the food and limited the effectiveness of consuming substantial quantities of unprocessed muscle tissue. This is a conservative estimate since the goat meat samples tested here were already partly processed, lacked cartilage and other mechanically demanding tissue, and were thus relatively unchallenging compared with most of the meat eaten during the Palaeolithic.

Lower Palaeolithic food processing techniques had marked but different effects on the ability to masticate USOs and meat (Table 2, Fig. 1 and Extended Data Tables 1–3). Slicing had no measurable effect on the mastication of USOs, but significantly reduced the average masticatory muscle recruitment used to consume meat by 12.7% per chew ($P < 0.05$) and 31.8% per sample ($P < 0.05$), and also reduced maximum particle size in the comminuted bolus by 40.5% ($P < 0.0001$). In contrast, pounding had no measured effect on the ability to masticate meat, but did reduce the average muscle recruitment used to consume USOs by 4.5% per chew ($P < 0.05$) and 8.7% per sample ($P < 0.05$).

Cooking, whenever it was adopted, would have led to further benefits. Roasted USOs required 14.1% less muscle recruitment per chew ($P < 0.05$) and 22.0% less per sample ($P < 0.05$) compared with unprocessed USOs, but were ready to be swallowed at 82.1% larger particle sizes ($P < 0.01$). Since USOs tend to be tough, force-limited foods[11,20,22], cooking would have substantially reduced hominin peak

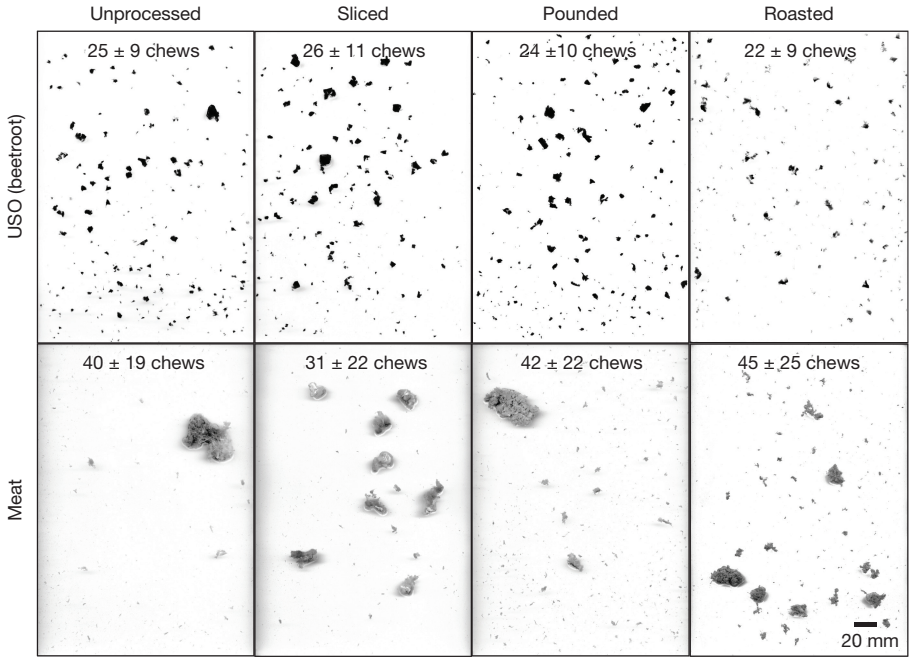

Figure 1 | Representative samples of chewed meat and USO (beetroot) boli before swallowing. Particles were dispersed so that they did not overlap. Average number of chews (±1 standard deviation (s.d.)) in parentheses ($n = 10$). Note that when meat is unprocessed (or to a lesser extent pounded) the bolus primarily consists of a single, unfractured food particle. Scale bar, 20 mm.

Table 2 | Effects of food processing on the mastication of USOs and meat

Food		Muscle recruitment* per chew (% change)	Muscle recruitment* per sample‡ (% change)	Comminution† (% change)
USOs	Sliced	NS	NS	NS
	Pounded	↓ 4.5%	↓ 8.7%	NS
	Roasted	↓ 14.1%	↓ 22.0%	↑ 82.1%
Meat	Sliced	↓ 12.7%	↓ 31.8%	↓ 40.5%
	Pounded	NS	NS	NS
	Roasted	↑ 15.3%	↑ 32.8%	↓ 47.1%

NS, not significant.
*Average percentage change of masticatory muscle recruitment (V.s) resulting from processing USOs (yam, carrot and beetroot data averaged) and meat. $N = 14$ (USOs) and 10 (meat). Only significant changes are shown. Significant changes relative to unprocessed samples are based on 95% confidence intervals greater or less than 0% change, studentized bootstrap (10,000 repeats).
†Participants chewed the food samples (unprocessed and processed beetroots and meat) until they felt the desire to swallow. The size of the largest particle in the chewed bolus was measured and the percentage change resulting from processing calculated. $N = 10$. Only significant changes are shown. Mixed linear models, $P \leq 0.05$.
‡Sum of muscular recruitment per chew used to consume each food sample.

masticatory effort, in turn reducing selection to maintain large teeth. Assuming that maximum bite force capabilities per chew scale with molar area to the power of 0.9 across primates[3], we can estimate that a 15% reduction in muscle recruitment resulting from roasting USOs would have allowed selection to reduce molar area by approximately 14%; a reduction nearly identical to the approximately 15% smaller post-canines of *H. sapiens* compared to *H. erectus*[4,27].

Roasting also substantially improves the ability to chew meat, although through a different mechanism than USOs. Roasting increased muscular effort by 15.3% per chew ($P < 0.05$) and 32.8% per sample ($P < 0.05$), but decreased the size of the largest particle by 47.1% ($P < 0.0001$), a reduction not significantly different from the effects of slicing meat ($P = 0.81$). In other words, roasted meat required more muscular effort per unit mass to chew, but resulted in a swallowable bolus with smaller particles because of more effective oral fracture.

To model the effects of meat consumption and processing on masticatory forces, we used estimated chewing forces (at the first molar) to predict total daily masticatory force for a hominin consuming 2,000 kcal day^{-1}. Although hominins ate many foods, we model the diet as different percentages of USOs and meat (Fig. 2). A diet composed entirely of unprocessed USOs would require approximately 40,000 chews per day. When unprocessed meat is added to the diet, masticatory demands per day decrease by approximately 156 chews and 0.5% of total chewing force for each additional percentage of calories from meat. Thus, if one-third of total calories derive from eating meat (a reasonable estimate based on modern African foraging societies[28]), a hominin would chew approximately 2 million fewer times per year (a 13% reduction) using 15% less total force than on a pure, unprocessed USO diet. If the meat were sliced, then hominins would not only reduce their masticatory effort by more than 2.5 million chews (a 17% reduction) and use 20% less force per year, but they would also swallow meat particles that were approximately 41% smaller, and thus more efficiently digestible[23] (see Tables 1 and 2).

Because the mechanical properties of foods vary depending on many factors such as species and type of portion consumed, further research is necessary to examine additional foods and processing techniques important to human evolution. More research is also needed to quantify the impacts of variations in masticatory morphology on chewing efficiency because dental topography and facial shape affect the relationship between food fracture and chewing effort (for example, sharper cusps increase applied chewing stresses, and relatively shorter jaws increase the mechanical advantage of the adductor muscles). Even so, we speculate that despite the many benefits of cooking for reducing endogenous bacteria and parasites[29], and increasing energy yields[23,24], the reductions in jaw muscle and dental size that

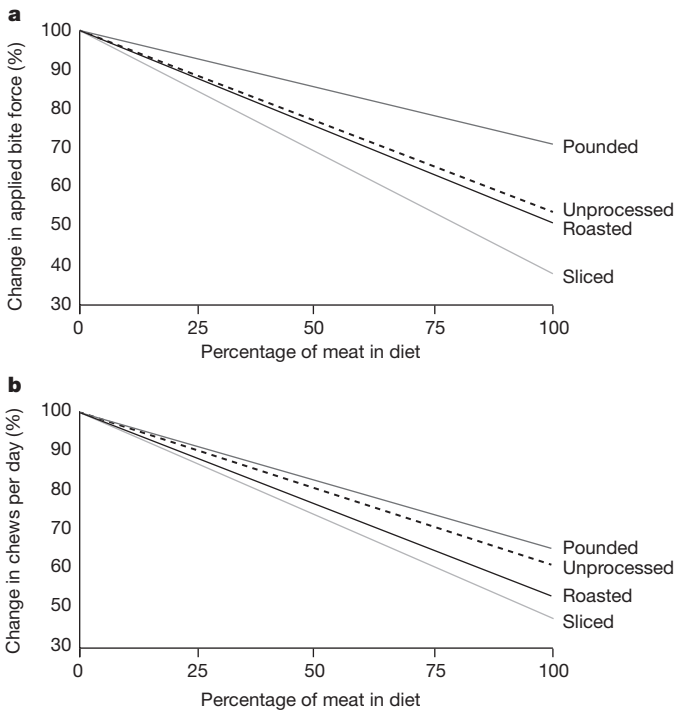

Figure 2 | Modelled effects of meat and food processing on mastication. **a**, **b**, Percentage change of applied masticatory force (kN.s) (**a**) and number of chews (**b**) used to consume a 2,000 kcal diet of unprocessed USOs (yam, carrot and beetroot data averaged) and varying amounts of meat that was unprocessed (dashed), sliced (light grey), pounded (dark grey), or roasted (black). Masticatory force was estimated from balancing-side-masseter EMG signals. Applied force and number of chews per kcal were calculated by dividing force or chews per sample by average sample weight and the foods' caloric density. Percentage change of total daily masticatory force and number of chews resulting from the inclusion of unprocessed and processed food was then calculated for diets ranging from 0% to 100% meat.

evolved by *H. erectus* did not require cooking and would have been made possible by the combined effects of eating meat and mechanically processing both meat and USOs. Specifically, by eating a diet composed of one-third meat, and slicing the meat and pounding the USOs with stone tools before ingestion, early *Homo* would have needed to chew 17% less often and 26% less forcefully. We further surmise that meat eating was largely dependent on mechanical processing made possible by the invention of slicing technology. Meat requires less masticatory force to chew per calorie than the sorts of generally tough plant foods available to early hominins, but the ineffectiveness of hominin molars to break raw meat would have limited the benefits of consuming meat before the invention of stone tools approximately 3.3 Ma. Although recent and contemporary hunter–gatherers are less dependent on stone tools than early *Homo* because they eat mostly cooked meat, many of the oldest tools bear traces of being used to slice meat[9], and the use of tools (now mostly metal knives) to process foods such as meat is well documented ethnographically[30]. This dependency on extra-oral mechanical processing, however, does not apply to other animal-based foods such as marrow, brains and visceral organs that might have been difficult to access without tools, but are easier to chew than muscle. Although it is possible that the masticatory benefits of food processing and carnivory favoured selection for smaller teeth and jaws in *Homo*, we think it is more likely that tool use and meat-eating reduced selection to maintain robust masticatory anatomy, thus permitting selection to decrease facial and dental size for other functions such as speech production, locomotion, thermoregulation, or perhaps even changes in the size and shape of the brain[16]. Whatever selection pressures favoured these shifts, however, they would not have been

possible without increased meat consumption combined with food processing technology.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to K.D.Z. (kzink@oeb.harvard.edu) or D.E.L. (danlieb@fas.harvard.edu).

METHODS

Experimental participants. Three experiments were performed (two on USOs, and one on meat). Experiment number 1 used 14 subjects (7 male, 7 female; aged 29 ± 8 years) to quantify the amount of masticatory muscular effort required to consume USOs. Experiment number 2 used 10 subjects (5 male, 5 female; aged 32 ± 10 years) to quantify comminution (intra-oral food breakdown) of one USO, beetroots. The dark colour of beetroots (but not yams and carrots) provided the colour contrast necessary to image and measure small food particles. Experiment number 3 used 10 male subjects (aged 36 ± 17 years) to quantify both the muscular effort required to consume meat, and how well the subjects were able to comminute the food. All participants had a complete set of permanent teeth with the exception of the third molars (which were variably present), possessed no major cavities, and reported no pain or difficulty during chewing. All experiments were approved by the Harvard Institutional Review Board (IRB), and all subjects provided informed consent before participation. No statistical methods were used to predetermine sample size.

Food samples. *USOs.* Organic USOs, jewel yams (*Ipomoea batatas*), carrots (*Daucus carota*), and red beetroots (*Beta vulgaris*), were purchased from a local grocery store. The average fracture toughness of these USOs is approximately 1,060 J m^{-2} (ref. 20), similar to published values from Africa of wild tubers (1,304 J m^{-2}), greater than wild bulbs (325 J m^{-2}) and corms (265 J m^{-2}), but less than wild rhizomes (5,448 J m^{-2}) (ref. 22). Each USO was cut into two portions; one was used for the unprocessed samples and the other for the processed samples. Unprocessed, sliced and pounded samples were prepared in a similar manner. First, small bite-sized cubes (13 mm × 13 mm × 13 mm) were cut from the inner medullary region of each USO. Sample dimensions were measured using digital callipers (accuracy ± 0.01 mm). Because of their small size, some of the carrot samples included a small portion of the outer cortex. Sample weight did not differ among the USOs (digital scale, accuracy ± 0.1 g; yam 2.2 ± 0.06 g; carrot 2.3 ± 0.05 g; beetroot 2.2 ± 0.06 g).

After the sample cubes were cut, they were either left unprocessed, or were processed by slicing them into eight smaller 6.5 mm × 6.5 mm × 6.5 mm cubes (sliced samples), or by pounding them six times with a hand-sized rock replica of a Lower Palaeolithic hammerstone (pounded samples). Tenderizing in this manner tended to break the USOs into many relatively large, intact pieces. Roasted samples were created by cutting the USOs into 17-mm-thick slices and then cooking them on a pre-heated tabletop propane grill (Perfect Flame) with the lid open and the gas flow valve set to 'high'. USO slices were roasted for 15 min, and to ensure uniform heating, they were flipped after 7.5 min and rotated every 2.5 min to different positions on the grill surface. Cooking in this manner heated yams to 89.0 ± 2.7 °C, carrots to 78.5 ± 1.1 °C, and beetroots to 78.6 ± 2.2 °C (based on the internal temperatures of 5 slices of each USO; Thermoworks thermometer, accuracy ± 0.1 °C). After cooking, 13 mm × 13 mm × 13 mm cubes were cut from the medullary region of the slices, avoiding the charred surfaces that were in contact with the grill. Cooked cubes were approximately 14% heavier than the unprocessed cubes (cooked yam 2.6 ± 0.05 g; cooked carrot 2.6 ± 0.05 g; cooked beetroot 2.6 ± 0.05 g). All samples were stored in sealed plastic containers at 4 °C and were used within 12 h of processing.

Meat. Fresh adult goat carcasses (*Capra aegagrus*; female) were purchased from a local farm (Blood Farms, Groton, Massachusetts) and transported on ice to the Skeletal Biology Laboratory, Harvard University. Neck and epaxial muscles (with little associated fat) were removed using aseptic procedures, sealed in vacuum bags and stored at −20 °C. Although freezing has a slight tenderizing effect[31,32], this step was required by the IRB to perform pathogen tests on the meat before using it in the experiment. The meat was defrosted slowly at 4 °C for approximately 12–24 h before sample preparation. Samples were randomized to include meat from both neck and epaxial muscles. Three-gram samples of meat were cut from defrosted muscles (digital scale, accuracy = 0.1 g). These samples were either left unprocessed, or were cut into eight, approximately equal sized pieces (sliced samples). Pounded samples were created by cutting the muscle into a 50.0 g steak and hitting it 50 times with a replica Lower Palaeolithic hammerstone. Processing in this manner disorganized the muscle fibres, resulting in a 'mashed' appearance, but did not fracture the steak into separate pieces. After tenderizing, 3.0 g samples were cut from the pounded steaks. Roasted samples were created by cooking steaks on the same grill used to cook USOs (see earlier for details). Internal temperature was monitored using a digital thermometer inserted into the steak centre (Thermoworks, accuracy ± 0.1 °C). Steaks were flipped regularly to ensure even heating and were roasted to a final internal temperature equal to medium-well done (slightly pink centre, ~70 °C). On average, cook time was 25.0 ± 5.3 min and water (weight) loss was 26.8 ± 5.6% when roasting in this manner (based on the average of three steaks). After roasting, 3.0 g samples were cut from the steaks, avoiding the charred outer surfaces. All samples were stored in sealed plastic containers at 4 °C and were used within 12 h of processing.

Order of presentation. In each of the experiments described later, subjects were presented with triplicate samples of the unprocessed and processed foods. While USO samples were presented in random order, owing to IRB restrictions the cooked meat samples were presented before the unprocessed, sliced and pounded meat samples (the latter three sample types were presented in random order). Additionally, although the subjects were allowed to swallow the USO samples, the risk of foodborne illness precluded swallowing of the non-cooked meat samples. We assessed the potential for bias that non-swallowing might cause by having the subjects chew six samples of cooked meat. Half of the samples were consumed as normal (chewed and swallowed), while the other half were chewed until the subjects felt they would typically swallow, and then spit out. There was no difference in the number of chews used (linear mixed models, $P = 0.65$) or muscle recruitment (linear mixed models, per chew $P = 0.20$, per sample $P = 0.99$). All of the data presented here are based on the cooked meat samples that were not swallowed.

Muscle recruitment and chewing forces. For each subject, surface electromyography (EMG) electrodes (Cleartrace, Conmed Corporation) were placed onto the skin overlying the major force-producing muscles of mastication, the right and left temporalis and masseter muscles, and a ground electrode was placed on the back of the non-dominant hand. EMG electrodes were connected to amplifiers (a pre-amplifier and amplifier; MA300 EMG system, Motion Lab Systems) and a PowerLab 16sp A/D board (ADinstruments). All data were collected at 1,000 Hz in LabChart v.7 (ADinstruments). (Temporalis muscle activity was not collected for 3 subjects in the USO experiment, and masseter muscle activity was not collected for 1 subject in the meat experiment.)

Experimental trials. After electrode placement, we calibrated each subject's EMGs with force. First, a small, dime-sized Kistler SlimLine force transducer (output voltage calibrated to known forces, $r^2 = 0.99$, for transducer details see later) was placed between the subjects' left first molars. The subjects were then instructed to bite down with sub-maximal force and then release while EMG activity and resulting bite forces were recorded. This procedure was repeated approximately 30 times over a range of bite forces (which were monitored in real time by K.D.Z.). To ensure a comfortable and sterile biting surface, the top and bottom of the transducer was fitted with a thin (2.4 mm) layer of rubber and was loosely covered with a layer of waterproof tape and a sterile plastic sleeve. After wrapping, the transducer was 8.8 mm tall with a diameter of 14.1 mm.

After the calibration trial, subjects were presented with unprocessed and processed foods in randomized order and instructed to chew the samples as normally as possible on only the left side, so that the balancing- and working-side muscles would be readily identifiable. During chewing, the EMG activity of each muscle was recorded. Two sets of analyses were performed: one that assessed the effects of food processing on chewing muscle recruitment, and one that estimated the applied forces necessary to fracture each food. The investigators were not blinded to allocation during experiments and outcome assessment.

Muscle recruitment analysis. The EMG signals were processed using custom Matlab codes. Specifically, the data were filtered (Butterworth bandpass; 4th order zero-lag; 60 and 300 Hz frequency cutoffs), rectified, binned with a 5 ms integral reset, and background EMG activity was removed using Thexton's randomization method[33]. Mid-trial swallows, which sometimes occurred during the consumption of the USO samples, were identified by non-uniform patterns of the muscle EMG signals and were omitted from analysis.

For each muscle, the time-integral of the EMG signal was calculated both per chew and per sample. The time-integral EMG data were then normalized within each subject by calculating the relative change in muscular recruitment caused when consuming processed versus unprocessed foods (percentage change = $100 \times ((\text{EMG voltage}_{\text{processed food}} - \text{EMG voltage}_{\text{unprocessed food}})/(\text{EMG voltage}_{\text{unprocessed food}}))$. Sample triplicates were averaged for each subject. Because the data were not normally distributed, we used 95% confidence intervals generated from studentized bootstraps[34] with 10,000 repeats to test whether food processing significantly increased (a positive value) or decreased (a negative value) muscle recruitment. (studentized bootstraps generate confidence intervals based on the resampled distribution of Student's *t*-tests.) EMG data were analysed for each muscle separately, and also with all of the muscles averaged. Similarly, USO data were analysed both for each specific USO (beetroot, carrot and yams), and with all of the USOs pooled together. All calculations were performed in Excel (Microsoft 2007) and R[35].

Chewing force analysis. To compare directly the masticatory effort used to chew USOs and meat, we transformed the time-integral EMG data of the balancing-side masseter into estimates of applied chewing force. Although we were not able to estimate the work done by chewing, the time-integral of estimated force is indicative of the total metabolic work done by the muscle, since the percentage of muscle work that generates force is relatively constant (about 25%). Standardization of

the EMG signals was necessary because USO and meat samples were different sizes, and EMG signals from different experiments can only be compared when they are normalized. The balancing-side masseter was used because Proeschel and Morneburg[36] found a different EMG–force relationship between isometric bites, such as those used in our calibration experiments, and chewing bites for all major masticatory muscles with the exception of the balancing-side masseter.

To estimate applied chewing forces, subject-specific calibration equations were calculated using the data collected during the calibration trials (see earlier) to transform each subject's muscle recruitment data into chew forces. Specifically, using methods described earlier, we filtered and rectified the balancing-side masseter EMG signal, and calculated the time-integral of the signal for each bite taken in the calibration trial. We then used LabChart v.7 to calculate the time-integral of the force signal used per bite (N.s). Each subject's force data were then regressed against their time-integral EMG data for each bite. Overall, the relationship between the time-integral of the balancing-side masseter EMG and the time-integral of measured bite force was strong and significant: the average R^2 ($\pm$ 1 s.d.) for all subject-specific calibration regressions was 0.73 ± 0.14; $P \leq 0.001$).

The subject-specific calibration equations generated by the regressions were then used to transform each subject's balancing-side masseter activity per chew into an estimate of applied masticatory force per chew. Total applied masticatory force per sample was then calculated by multiplying the average applied force per chew by the number of chews that a subject used to consume the food.

Finally, the average masticatory force and number of chews used per kcal of each food sample was calculated by dividing by the weight of each sample and the number of calories available per gram of food (see Table 1). All meat samples weighed 3.0 g and USO samples weighed an average of 2.2 g when unprocessed and sliced, 2.1 g when pounded, and 2.6 g when roasted. Food caloric density was obtained from the USDA National Nutrient Database for Standard Reference (http://www.ars.usda.gov/ba/bhnrc/ndl): unprocessed jewel yam = 0.86 kcal g^{-1}; unprocessed red beetroot = 0.43 kcal g^{-1}; unprocessed carrot = 0.41 kcal g^{-1}; unprocessed goat meat = 1.09 kcal g^{-1}; baked jewel yam = 0.90 kcal g^{-1}; boiled red beetroot = 0.44 kcal g^{-1}; boiled carrot = 0.35 kcal g^{-1}; roasted goat = 1.43 kcal g^{-1}. Caloric data were unavailable for roasted USOs, and baked or boiled USO values were substituted in the calculations. Sliced and pounded foods were assumed to have the same number of calories per gram as their unprocessed counterparts. Yam, carrot and beetroot data were pooled and the average masticatory force per kcal of USO was calculated. A two-tailed Mann–Whitney *U*-test was used to assess whether the number of chews and masticatory force used to eat a kilocalorie of food differed between USOs and meat. All calculations were performed in Excel (Microsoft 2007) and StatView (SAS Institute). Significance was set to $P \leq 0.05$.

It should be noted that the caloric values used in these calculations are based on the Atwater system, which calculates food energy as the total available energy minus the indigestible components. This system assumes a standard digestibility, however, and also fails to take into account other key variables, such as the cost of digestion, which is lower in processed foods[23,24]. Therefore, these caloric data probably under-report the net energy gained from processed foods.

Comminution. Subjects were instructed to chew the meat and USO (beetroot) samples on the left side of their mouth until they felt that they would typically swallow. At this point they stopped chewing and the food bolus was collected in 50 ml tubes and stored in ~50% ethanol for no more than 8 days before image analysis.

Particle size analysis. Comminuted boli were dispersed onto a transparent plastic tray fitted onto an Epson perfection v500 flatbed scanner. Food particles comprising each bolus were easily separated using water, and were arranged so that the particles did not touch one another and to maximize surface area contact with the tray. Particles were then scanned to create a 400 dpi grey-scale image against a white background. Images were viewed and measured in iVision v.4 (BioVision Technologies).

Comminution effectiveness was quantified as the two-dimensional surface area of the largest particle of food within the chewed bolus. We use this variable rather than average particle size because the chewed boli of unprocessed meat were predominantly composed of a single large particle, making average size uninformative (see Fig. 1). In most instances, the largest particle in a chewed meat bolus was readily identifiable in the scanned images. Using the drawing tool, the pixels comprising the largest particle were manually transformed into the measurement colour (green), and the total two-dimensional surface area (mm^2) of the particle was then quantified based on the number of coloured pixels. In some samples, multiple particles had to be measured to locate the largest particle. In contrast to meat, the comminuted USO samples contained a large number of similarly sized particles, and it was not possible to discern the largest particle simply by viewing the scanned images. Therefore, all of the particles that made up the sample were measured. To do this, the scanned image was thresholded so that every coloured pixel with a value ranging from 0 to 230 (pure black to very light grey, respectively) was transformed into the measurement colour (green). (Preliminary tests indicated that thresholding to 230 was the boundary between very small, light particles and shadows resulting from the scanner's moving light source.) After thresholding, the image was reviewed and digitally cleaned by hand if needed. The surface area of every individual food particle was measured by quantifying the number of green pixels comprising the particle (a single particle was defined as the sum of all green pixels in contact). For consistency, we report only data on the size of the largest particle in the chewed USO boli, which correlated strongly with average particle size ($r = 0.73$; $P < 0.0001$) (see Extended Data Table 1).

Triplicates of each sample type were averaged, and the size of the largest particle in raw and processed comminuted samples was compared using linear mixed models, a type of model that estimates separate intercepts for each subject[37]. All calculations were performed in Excel (Microsoft 2007) and R[35]. Significance was set to $P \leq 0.05$. Measurement precision was quantified by measuring the bolus of one randomly chosen sample (unprocessed meat) five times. The standard deviation of the resulting measurements (1.4 mm^2) was 0.2% that of the average particle area (542.6 mm^2). The maximum difference between any two repeats was 0.5% of the average.

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Extended Data Table 1 | The number and size of food particles contained within chewed USO (beetroot) and meat boli at 'swallow'

Food		Particle Size (mm^2)			Total Surface Area (mm^2)	Number of Particles
		Largest	*Median*	*Average*		
USOs (Beets)	*Unprocessed*	38.52 (26.39)	0.22 (0.09)	1.23 (0.41)	1593.28 (423.47)	1434.10 (635.19)
	Sliced	33.05 (17.49)	0.26 (0.10)	1.37 (0.65)	1594.36 (399.07)	1367.60 (637.73)
	Pounded	31.87 (17.04)	**0.29 (0.07)**	**1.49 (0.58)**	1567.62 (412.09)	1159.50 (454.40)
	Roasted	**57.36 (24.90)**	**0.30 (0.08)**	**2.08 (0.62)**	1922.87 (406.84)	1061.30 (653.39)
Meat	*Unprocessed*	697.3 (207.9)				
	Sliced	**363.6 (108.8)**				
	Pounded	759.5 (136.7)				
	Roasted	**378.8 (183.3)**				

Subjects chewed unprocessed and processed USOs (beetroots) and meat until they felt that they would typically swallow. The chewed bolus was collected and the two-dimensional surface area of the particles comprising the bolus measured. $N = 10$. Average values are shown. One standard deviation in parentheses. Bold values indicate a significant difference between processed and unprocessed foods. Mixed linear models, $P \leq 0.05$.

Extended Data Table 2 | Average percentage change of chewing muscle recruitment per chew when masticating size-standardized processed USOs and meat, relative to unprocessed samples

Food		**Balancing Side** (% Change)		**Working Side** (% Change)		**Muscle Average** (% Change)
		Masseter	*Temporalis*	*Masseter*	*Temporalis*	
Yam (*N=14*†)	*Sliced*	0.1 (9.5) *95% CI: 6 to -5*	3.6 (8.9) *95% CI: 9 to -4*	-0.3 (10.7) *95% CI: 5 to -8*	3.4 (9.4) *95% CI: 12 to -1*	**0.8 (5.6)** *95% CI: 3 to -4*
	Pounded	-4.9 (10.1) *95% CI: 2 to -10*	-2.2 (12.0) *95% CI: 10 to -8*	-0.9 (19.8) *95% CI: 14 to -10*	0.2 (10.7) *95% CI: 14 to -5*	**-2.3 (9.9)** *95% CI: 7 to -7*
	Roasted	-24.2 (14.8) *95% CI: -14 to -32*	-32.1 (13.6) *95% CI: -22 to -44*	-25.7 (13.0) *95% CI: -15 to -32*	-30.7 (15.4) *95% CI: -15 to -39*	**-27.3 (14.7)** *95% CI: -15 to -34*
Carrot (*N=14*†)	*Sliced*	-0.2 (8.9) *95% CI: 6 to -5*	-1.4 (10.3) *95% CI: 5 to -9*	-0.6 (10.0) *95% CI: 5 to -7*	4.0 (14.3) *95% CI: 16 to -4*	**0.7 (8.8)** *95% CI: 6 to -4*
	Pounded	-8.7 (13.3) *95% CI: -1 to -17*	-6.1 (10.3) *95% CI: 0.2 to -15*	-3.5 (8.8) *95% CI: 1 to -11*	-2.3 (13.1) *95% CI: 7 to -11*	**-4.4 (8.7)** *95% CI: -0.1 to -11*
	Roasted	-7.3 (7.9) *95% CI: -1 to -11*	-9.7 (8.2) *95% CI: -5 to -20*	-13.3 (9.9) *95% CI: -8 to -20*	-6.2 (9.3) *95% CI: -2 to -17*	**-9.7 (6.2)** *95% CI: -6 to -14*
Beet (*N=14*†)	*Sliced*	-3.1 (14.9) *95% CI: 5 to -13*	2.4 (7.8) *95% CI: 7 to -3*	8.3 (28.8) *95% CI: 53 to -3*	-2.8 (8.7) *95% CI: 4 to -8*	**-0.2 (8.3)** *95% CI: 5 to -4*
	Pounded	-11.9 (15.5) *95% CI: -3 to -21*	-7.0 (10.1) *95% CI: -1 to -15*	-4.4 (8.9) *95% CI: 1 to -9*	-7.6 (7.2) *95% CI: -3 to -14*	**-6.8 (7.6)** *95% CI: -2 to -11*
	Roasted	-4.1 (8.0) *95% CI: 0.2 to -9*	-2.3 (6.1) *95% CI: 1 to -7*	-6.3 (14.8) *95% CI: 0.4 to -20*	-4.8 (7.5) *95% CI: -0.5 to -11*	**-5.4 (6.8)** *95% CI: -2 to -10*
USO Average	*Sliced*	-1.1 (7.6) *95% CI: 3 to -8*	1.5 (4.4) *95% CI: 4 to -3*	2.4 (10.2) *95% CI: 12 to -2*	1.5 (5.4) *95% CI: 5 to -2*	**0.5 (3.4)** *95% CI: 2 to -2*
	Pounded	-8.5 (9.1) *95% CI: -3 to -13*	-5.1 (8.0) *95% CI: 1 to -10*	-3.0 (7.9) *95% CI: 3 to -7*	-3.2 (7.4) *95% CI: 2 to -8*	**-4.5 (6.1)** *95% CI: -0.01 to -7*
	Roasted	-11.9 (6.9) *95% CI: -7 to -15*	-14.7 (6.9) *95% CI: -10 to -19*	-15.1 (10.0) *95% CI: -10 to -23*	-13.9 (7.6) *95% CI: -8 to -19*	**-14.1 (6.8)** *95% CI: -9 to -18*
Meat (*N=10*‡)	*Sliced*	-13.8 (15.0) *95% CI: 3 to -24*	-14.3 (14.3) *95% CI: -5 to -26*	-12.0 (9.9) *95% CI: -6 to -22*	-11.1 (10.3) *95% CI: -3 to -18*	**-12.7 (10.1)** *95% CI: -5 to -20*
	Pounded	13.5 (12.9) *95% CI: 23 to 2*	8.6 (16.5) *95% CI: 23 to -2*	8.3 (14.5) *95% CI: 18 to -6*	5.2 (11.5) *95% CI: 14 to -3*	**7.9 (12.6)** *95% CI: 18 to -1*
	Roasted	24.4 (21.3) *95% CI: 42 to 9*	12.0 (18.2) *95% CI: 32 to 1*	17.7 (24.3) *95% CI: 51 to 3*	12.5 (17.2) *95% CI: 38 to 4*	**15.3 (18.1)** *95% CI: 40 to 6*

For each food, muscle recruitment percentage change = $100 \times ((\text{EMG voltage per chew}_{\text{processed food}} - \text{EMG voltage per chew}_{\text{unprocessed food}})/(\text{EMG voltage per chew}_{\text{unprocessed food}}))$. One standard deviation in parentheses. Significant changes relative to unprocessed samples are shaded grey based on 95% confidence intervals (CI) greater or less than 0% change, studentized bootstrap (10,000 repeats).
*The temporalis muscle was not collected from 3 subjects, reducing samples size to 11 for this muscle.
†The masseter muscle was not collected from 1 subject, reducing sample size to 9 for this muscle.

Extended Data Table 3 | Average percentage change of chewing muscle recruitment per sample when masticating size-standardized processed USOs and meat, relative to unprocessed samples

Food		Balancing Side (% Change)		Working Side (% Change)		Muscle Average (% Change)
		Masseter	*Temporalis*	*Masseter*	*Temporalis*	
Yam (*N=14*[‡])	*Sliced*	3.1 (10.5) *95% CI: 8 to -5*	6.6 (11.8) *95% CI: 18 to 1*	2.4 (10.0) *95% CI: 10 to -2*	6.7 (13.7) *95% CI: 17 to -2*	**3.8 (9.4)** *95% CI: 9 to -2*
	Pounded	-13.1 (15.8) *95% CI: -2 to -21*	-11.1 (17.0) *95% CI: 4 to -21*	-10.0 (18.3) *95% CI: -1 to -23*	-9.0 (17.3) *95% CI: 3 to -19*	**-10.9 (16.1)** *95% CI: -1 to -19*
	Roasted	-42.0 (20.2) *95% CI: -27 to -52*	-49.9 (16.8) *95% CI: -36 to -60*	-43.6 (19.1) *95% CI: -30 to -53*	-48.3 (19.8) *95% CI: -25 to -59*	**-44.3 (20.1)** *95% CI: -28 to -54*
Carrot (*N=14*[‡])	*Sliced*	2.4 (12.1) *95% CI: 10 to -4*	-0.8 (10.5) *95% CI: 6 to -8*	2.7 (15.9) *95% CI: 16 to -4*	4.7 (13.5) *95% CI: 16 to -3*	**3.5 (13.2)** *95% CI: 15 to -2*
	Pounded	-9.9 (16.4) *95% CI: 2 to -18*	-10.5 (12.4) *95% CI: -1 to -17*	-4.1 (17.8) *95% CI: 8 to -13*	-6.6 (14.3) *95% CI: 3 to -16*	**-5.4 (14.9)** *95% CI: 5 to -13*
	Roasted	-13.6 (10.1) *95% CI: -7 to -19*	-17.3 (14.5) *95% CI: -7 to -26*	-17.6 (16.0) *95% CI: -5 to -25*	-13.5 (16.9) *95% CI: 1 to -23*	**-15.0 (13.0)** *95% CI: -5 to -21*
Beet (*N=14*[‡])	*Sliced*	4.1 (27.3) *95% CI: 25 to -8*	11.6 (23.9) *95% CI: 33 to -0.1*	14.6 (35.4) *95% CI: 83 to -1*	5.8 (23.7) *95% CI: 30 to -6*	**6.8 (22.8)** *95% CI: 27 to -2*
	Pounded	-14.8 (17.2) *95% CI: -4 to -25*	-9.5 (16.1) *95% CI: 1 to -20*	-8.1 (13.1) *95% CI: 3 to -14*	-9.8 (14.8) *95% CI: -0.4 to -20*	**-9.9 (13.3)** *95% CI: -1 to -17*
	Roasted	-5.8 (14.0) *95% CI: 2 to -14*	-4.0 (13.2) *95% CI: 6 to -12*	-7.1 (22.2) *95% CI: 4 to -22*	-6.6 (14.8) *95% CI: 5 to -15*	**-6.7 (14.9)** *95% CI: 2 to -15*
USO Average	*Sliced*	3.2 (12.8) *95% CI: 10 to -4*	5.8 (11.7) *95% CI: 15 to -1*	6.6 (14.2) *95% CI: 21 to 0.3*	5.7 (13.3) *95% CI: 17 to -2*	**4.7 (11.0)** *95% CI: 11 to -1*
	Pounded	-12.6 (12.5) *95% CI: -4 to -19*	-10.4 (12.2) *95% CI: 3 to -17*	-7.4 (10.0) *95% CI: 0.3 to -12*	-8.5 (11.5) *95% CI: -0.1 to -16*	**-8.7 (10.8)** *95% CI: -0.4 to -14*
	Roasted	-20.5 (9.3) *95% CI: -15 to -26*	-23.8 (10.0) *95% CI: -17 to -31*	-22.8 (13.5) *95% CI: -16 to -32*	-22.8 (11.4) *95% CI: -15 to -30*	**-22.0 (10.5)** *95% CI: -16 to -28*
Meat (*N=10*[§])	*Sliced*	-29.2 (36.1) *95% CI: 5 to -52*	-33.3 (30.4) *95% CI: -8 to -52*	-29.3 (31.3) *95% CI: -2 to -51*	-30.7 (31.9) *95% CI: -2 to -49*	**-31.8 (31.2)** *95% CI:-5 to -50*
	Pounded	28.1 (42.2) *95% CI: 58 to -7*	19.8 (44.1) *95% CI: 53 to -12*	24.2 (40.2) *95% CI: 52 to -15*	15.4 (38.6) *95% CI: 45 to -12*	**18.7 (40.9)** *95% CI: 48 to -12*
	Roasted	42.8 (56.9) *95% CI: 100 to 6*	28.4 (52.0) *95% CI: 85 to 1*	37.4 (61.2) *95% CI: 98 to -2*	29.5 (47.8) *95% CI: 75 to 1*	**32.8 (51.7)** *95% CI: 82 to 3*

Chewing muscle recruitments per sample were calculated as the sum of muscular recruitment per chew used to consume each food sample. For each food, muscle recruitment percentage change = $100 \times ((\text{EMG voltage per sample}_{\text{processed food}} - \text{EMG voltage per sample}_{\text{unprocessed food}})/(\text{EMG voltage per sample}_{\text{unprocessed food}}))$. One standard deviation in parentheses. Significant changes relative to unprocessed samples are shaded grey based on 95% confidence intervals (CI) greater or less than 0% change, studentized bootstrap (10,000 repeats).
*The temporalis muscle was not collected from 3 subjects, reducing samples size to 11 for this muscle.
†The masseter muscle was not collected from 1 subject, reducing sample size to 9 for this muscle.