

RESEARCH ARTICLE

In vitro strain in human metacarpal bones during striking: testing the pugilism hypothesis of hominin hand evolution

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ABSTRACT

The hands of hominins (i.e. bipedal apes) are distinguished by skeletal proportions that are known to enhance manual dexterity but also allow the formation of a clenched fist. Because male–male physical competition is important in the mating systems of most species of great apes, including humans, we tested the hypothesis that a clenched fist protects the metacarpal bones from injury by reducing the level of strain during striking. We used cadaver arms to measure *in vitro* strain in metacarpals during forward strikes with buttressed and unbuttressed fist postures and during side slaps with an open palm. If the protective buttressing hypothesis is correct, the clenched fist posture should substantially reduce strain in the metacarpal bones during striking and therefore reduce the risk of fracture. Recorded strains were significantly higher in strikes in which the hand was secured in unbuttressed and slapping postures than in the fully buttressed posture. Our results suggest that humans can safely strike with 55% more force with a fully buttressed fist than with an unbuttressed fist and with twofold more force with a buttressed fist than with an open-hand slap. Thus, the evolutionary significance of the proportions of the hominin hand may be that these are the proportions that improved manual dexterity while at the same time making it possible for the hand to be used as a club during fighting.

KEY WORDS: Male–male competition, Sexual selection, Fighting, Great ape, Hominidae, Fist

INTRODUCTION

The human hand presents a biomechanical paradox. It is critical to most human behaviors: foraging for, preparing and ingesting food; crafting and using tools; building shelter; playing musical instruments; producing art; communicating complex intentions and emotions; and nurturing. The capacity for precise and delicate manipulation requires that the hand be a relatively fragile and vulnerable part of our musculoskeletal system. Yet, the hand is also our most important anatomical weapon, used as a club to threaten, beat and sometimes kill other humans. These seemingly incompatible uses have recently been suggested to be the result of specialization of the hominin hand for both manual dexterity and punching (Morgan and Carrier, 2013). The hypothesis that the proportions of the hominin hand are, in part, the result of selection acting on fighting behavior is controversial (King, 2013; Nickle and Goncharoff, 2013) and has implications for the role that male–male physical competition has played in the evolution of the hominin lineage (Daly and Wilson, 1988, 1999a,b; Wrangham and Peterson,

1996; Puts, 2010; Puts et al., 2012; Sell et al., 2009, 2012; Carrier, 2011; Morgan and Carrier, 2013; Carrier and Morgan, 2015).

In comparison to those of the last common ancestor of chimpanzees and humans, the hands of hominins have shorter palms and fingers, but longer thumbs (Almécija et al., 2015). Human-like manual proportions were present in basal hominins, the australopiths (Almécija et al., 2010; Alba et al., 2003; Susman, 1994, 1988; Kivell et al., 2011). These hand proportions are generally thought to be crucial to the great manipulative skills of humans and are usually associated with tool manufacture and use (Napier, 1962; Marzke, 1997; Susman, 1998; Young, 2003; Almécija et al., 2010, 2015). Recently, many of the derived proportions of the hominin hand have also been suggested to be a pleiotropic result of selection on the foot for terrestrial locomotion (Alba et al., 2003; Rolian et al., 2010). There are clear arguments suggesting that both of these factors played a role in the evolution of hominin hand proportions. Regardless, these two hypotheses are compatible with the possibility that the proportions of the hominin hand are, at some level, also the result of sexual selection on punching performance during hand-to-hand fighting.

The relatively high frequency of metacarpal bone fractures sustained during fighting (Gudmundsen and Borgen, 2009; Jeanmonod et al., 2011) has been used to argue that the hand is too delicate to have evolved to be a weapon (King, 2013). However, the primary target during fistfights is the face (Shepherd et al., 1990; Boström, 1997; Brink et al., 1998; Le et al., 2001), and bones of the face break much more frequently during fights than do bones of the hand, indicating that the fist is an effective weapon (Carrier and Morgan, 2015). Nevertheless, the high frequency of metacarpal fractures represents a challenge to the protective buttressing hypothesis and raises the possibility that a clenched fist does not reduce the risk of injury to these bones.

The hominin fist may reduce peak loads on the metacarpals during striking through a transfer of energy from digits 2 and 3 to the adductor muscles of the thumb and through the thumb to the wrist (Morgan and Carrier, 2013) (Fig. 1). To test the prediction that the clenched fist posture of hominin hands protects the metacarpal bones against fracture during punching, we measured *in vitro* strain in these bones during forward strikes with buttressed and unbuttressed fist postures and during side slaps with an open-palm posture. If the protective buttressing hypothesis is correct, the clenched fist posture is expected to substantially reduce strain in the metacarpal bones during striking and therefore reduce the risk of fracture.

RESULTS

During forward strikes, the metacarpals were loaded in long-axis bending in both the buttressed and unbuttressed postures. The dorsal surface of the second, third and fifth metacarpal diaphyses exhibited tensile strain (Tables 1–4). In contrast, we observed compressive strains in the ventral diaphyseal surface (Tables 2, 4). The second

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Fig. 1. Illustration of the hypothesized transfer of energy during a strike from digits 2 and 3 to the adductor muscles of the thumb and through the thumb to the wrist. The gray lines illustrate the posture of the digits before impact and the black lines the posture immediately after impact. During impact, the force (gray arrows) applied to the proximal phalanges of digits 2 and 3 produces flexion at the metacarpo-phalangeal joints. Flexion of these digits transfers force to the thenar eminence abducting the first metacarpal. Through this linkage, we hypothesize that force (black arrow) is transferred through the first metacarpal to the wrist and energy is dissipated as a result of stretching of the adductor and flexor muscles of the thenar eminence and thumb. Reproduced from Morgan and Carrier, 2013.

metacarpal specimen (no. 1), which we instrumented with a rosette strain gauge, showed that the orientation of the principle strain on the dorsal diaphysis was closely aligned with the long axis of the bone, varying by only 3.40 ± 6.00 deg (mean \pm s.d., $N=20$) from the long axis during both buttressed and unbuttressed forward strikes. During slapping strikes, the dorsal surface of the second metacarpal was loaded in compression (Tables 1, 3).

The level of diaphyseal strain was dependent on striking mode. Fig. 2 plots an example of peak strain versus peak force for slaps and unbuttressed and buttressed forward strikes. Strain in the dorsal diaphyses was significantly higher in unbuttressed than in buttressed strikes in the seven second metacarpal specimens and in the third and fifth metacarpal specimens (Tables 1–4, Fig. 3). The average striking strain/force ratio recorded on the dorsal diaphysis of the second metacarpal increased by $55.4 \pm 33.2\%$ ($N=7$, $P=0.0023$) when the fist posture was switched from buttressed to unbuttressed. Although the sample size was small, strain/force ratios for slapping trials were much greater than ratios for buttressed strikes, with an

average increase in strain relative to that of buttressed forward strikes of $103.0 \pm 83.3\%$ ($N=3$).

DISCUSSION

The bone strains recorded in this study were well below those that cause bone to fail. Tensile yield strain of human femur cortical bone, for example, has been reported to average 0.73% (Bayraktar et al., 2004), whereas the peak strains we imposed on the metacarpals were approximately 0.1%, or 1000 microstrains (μ strains). Nevertheless, if we extrapolate our results to strain levels that do cause bone failure, humans could safely strike on average with 55% more force with a fully buttressed fist than with an unbuttressed fist and with twofold more force with a buttressed fist than with an open-hand slap. Thus, a fully clenched fist does appear to provide significant protection to the metacarpal bones when the hand is used to strike.

A common misconception among anthropologists is that little evidence exists for fighting with fists in human history and prehistory. In actuality, the historical record indicates that the use of fists to strike an opponent was common in many human cultures, including the Chinese Xia dynasty (2100–1600 BCE; Henning, 1997), Mesopotamia (3000–1000 BCE; Murray, 2010); Thebes, Egypt (1350 BCE; Murray, 2010), Greece (eighth century BCE; Powell, 2014), Hausa people of the Sahel region of Africa (Gems, 2014), and the Aymara and Quechua people of the Andes (Lessa and Mendonça de Souza, 2006). The ethnography literature also contains many examples, from around the world, of males fighting with their fists (de CocCola and King, 1955; Balıkcı, 1989; Shimkin, 1990; Scott and Buckley, 2014; Tausk, 2010; Chagnon, 2013; Walker, 1997; Draper, 1978). Traumatic injuries in prehistoric skeletal samples are a direct source of evidence for testing hypotheses of interpersonal violence (Walker, 2001). Modern assault injuries resulting from fist strikes show a distinctive distribution of skeletal injuries with high rates of trauma to the face (Walker, 1997, 2001; Carrier and Morgan, 2015). Facial skeletal trauma consistent with injury due to fist fighting has been observed in many samples of prehistoric skeletal remains (Owens, 2007; Cohen et al., 2012; Judd, 2004; Jurmain, 2001; Jurmain et al., 2009; Andrushko and Torres, 2011; Lessa and Mendonça de Souza, 2004; Standen and Arriaza, 2000; Scott and Buckley, 2014; Walker, 1997; Webb, 2009). Additionally, evidence consistent with facial skeletal trauma due to fist fighting also exists in the fossil record of *Australopithecus* (Dart, 1948; Roper, 1969) and early *Homo* (Wu et al., 2011; Pérez et al., 1997; Curnoe and Brink, 2010).

The importance of a clenched fist to human aggression is also reflected in the role that it plays in threat displays. Game theory modeling of aggressive encounters suggests that threat displays

Table 1. Mean ratio of the peak striking strain to peak striking force (μ strain N^{-1}) recorded by strain gauges attached to the dorsal diaphysis of the second metacarpal

Arm	Buttressed		Unbuttressed		Slap		P-value	
	Mean \pm s.d.	N	Mean \pm s.d.	N	Mean \pm s.d.	N	B–UB	B–S
1	3.23 \pm 0.48	10	4.99 \pm 0.57	10	–	–	<0.0001	–
2	2.63 \pm 0.55	11	3.69 \pm 0.82	10	–	–	0.00340	–
3	5.12 \pm 0.14	10	6.09 \pm 0.46	11	–	–	<0.0001	–
4	1.14 \pm 0.15	12	1.31 \pm 0.05	9	–	–	0.00177	–
5	–	–	2.58 \pm 0.38	16	–4.14 \pm 1.02	18	–	–
6	1.32 \pm 0.08	14	2.56 \pm 0.61	12	–4.49 \pm 0.91	13	<0.0001	<0.0001
7	3.85 \pm 0.63	16	6.46 \pm 1.82	16	–5.33 \pm 1.80	14	<0.0001	0.0103
8	2.67 \pm 0.68	15	5.28 \pm 0.78	17	–7.93	19	<0.0001	<0.0001

B, buttressed; UB, unbuttressed; S, slap.

Table 2. Mean ratio of the peak striking strain to peak striking force ($\mu\text{strain N}^{-1}$) recorded by strain gauges attached to the surface of the ventral diaphysis of the second metacarpal and to the dorsal surface of the third and fifth metacarpals

Arm	Surface/bone	Buttressed		Unbuttressed		P-value
		Mean \pm s.d.	N	Mean \pm s.d.	N	
3	MC2, ventral	-4.52 \pm 0.40	10	-5.52 \pm 0.16	11	<0.0001
2	MC5, dorsal	2.16 \pm 0.83	14	4.21 \pm 1.34	12	0.0002
3	MC3, dorsal	3.82 \pm 0.17	12	5.69 \pm 1.03	9	0.0006

provide an honest indication of one's fighting ability (Maynard Smith and Price, 1973; Parker, 1974; Enquist, 1985; Szamado, 2008; Szalai and Szamado, 2009). Threat displays provide clues to the weapons used in fighting; these displays are usually the first step in a species' fighting technique that is used to threaten (Szamado, 2008; Walther, 1984). Thus, it is noteworthy that a number of researchers have suggested that the formation of a fist in response to stressful stimuli reflects a willingness to use physical force to resolve disputes (Darwin, 1899; Ekman, 1993; Schubert and Koole, 2009; Morris, 1977; Crowner et al., 2005). Human infants often use a 'closed hand' to express distress (Legerstee et al., 1990). When anger is associated with a desire to attack an offender, the facial expression of an open, 'square' mouth with the teeth showing is often associated with clenched fists (Ortony and Turner, 1990). These observations are consistent with the suggestion that fighting with fists is an innate human behavior.

Support for the hypothesis that selection on fighting influenced the evolution of human hand proportions is also found in the etymology of the Proto-Indo-European language, the reconstructed common ancestor of the Indo-European languages, which appears to date back to the mid-Neolithic, 6000–4000 BCE (Gamkrelidze and Ivanov, 1990; Mallory, 1989). The English word 'arm', referring to the forelimb of humans, is derived from the Proto-Indo-European 'arəm' which is a cognate of the Proto-Indo-European word for weapon 'armo' (Partridge, 1958; Klein, 1971; Watkins, 2000). Thus, weapons, from clubs to nuclear missiles, are commonly referred to as 'arms' or 'armaments'; and preparation for combat involves 'arming' oneself. The English word 'pugnacious' is derived from the Latin 'pugnō', meaning 'I fight', which is derived from the Proto-Indo-European 'puǵno-', meaning 'fist' (Partridge, 1958; Klein, 1971; Watkins, 2000). Similarly, 'impugn' is derived from the Latin 'impugno', which is also from the Proto-Indo-European 'puǵno-' (Partridge, 1958; Klein, 1971; Watkins, 2000). The observation that the ancient Proto-Indo-Europeans formed a linguistic connection between weapons and the human forelimb, and between aggressive behavior and the human fist suggests that the forelimb and fist played a central role in the aggressive behavior of early *Homo sapiens*.

Regardless of the extent to which *Homo sapiens* fight with their fists, it is important to remember that the skeletal proportions that allow a clenched fist were present in basal hominins (Almécija et al., 2010; Alba et al., 2003; Susman, 1994, 1988; Kivell et al., 2011). If the hand evolved to be a more effective weapon in early hominins, it is reasonable to expect co-evolution of protective buttressing in the face (Nickle and Goncharoff, 2013), the primary target when humans fight hand-to-hand. A review of the literature shows that the facial bones that most often fracture when struck by a fist (mandible, zygoma, nasals, bones of the orbit and mastoid) are also the parts of the skull that exhibited the greatest increase in robustness in australopiths (Carrier and Morgan, 2014). These same facial bones also show the greatest levels of sexual dimorphism in the skulls of both australopiths and *Homo*. One aspect of the human face appears inconsistent with the protective buttressing hypothesis – the vulnerable protuberant nose. This inconsistency may be related to the suggestion that the nose of *Homo* evolved as an amplifier signal of individual quality (Mikalsen et al., 2014). Nevertheless, the derived facial features of early hominins, the australopiths, appear to be fully consistent with the evolution of protective buttressing of the facial skeleton for fighting with fists.

Relative to other mammals, primates are recognized as being specialized for manual dexterity. Of significance to this study is the recent finding that the last common ancestor of chimpanzees and humans appears to have had a high thumb-to-digit length ratio more similar to that of humans than chimpanzees (Almécija et al., 2015). (However, see analyses presented in supplementary material figs S7 and S8 of Almécija et al., 2015 that suggest hominins and chimps are more equally divergent from the last common ancestor.) A high thumb-to-digit ratio is required for the pad-to-pad precision grip of humans (Napier, 1962; Marzke, 1997) and was acquired convergently in hominins with two other highly dexterous anthropoids, *Cebus* and *Theropithecus* (Almécija et al., 2015). Although the thumb-to-digit ratios of *Cebus* and *Theropithecus* are more or less identical to those of hominins, the length proportions of the skeletal elements in the digital rays differ from those of humans in ways that may not be fully compatible with phalangeal–palmar buttressing of the fist (Morgan and Carrier, 2013). Compared with hominins, *Theropithecus* has relatively long metacarpals and short

Table 3. Slopes and correlation coefficients of least-squared regressions of peak strain (μstrain) versus peak force (N) recorded during forward strikes from strain gauges attached to the dorsal diaphysis of the second metacarpal bone

Arm	Buttressed			Unbuttressed			Slap			P-value	
	Slope	R ²	N	Slope	R ²	N	Slope	R ²	N	B–UB	B–S
1	2.38	0.82	10	3.85	0.97	10	–	–	–	0.0047	–
2	2.01	1.00	11	2.79	1.00	10	–	–	–	0	–
3	4.89	1.00	10	6.91	0.99	11	–	–	–	<0.0001	–
4	0.89	0.97	12	1.36	0.99	9	–	–	–	<0.0001	–
5	–	–	–	1.79	0.92	16	-2.36	0.59	18	–	0.278
6	1.40	0.99	14	3.04	0.97	12	-4.82	0.80	13	<0.0001	<0.0001
7	2.91	0.93	16	4.19	0.99	16	-2.54	0.89	14	<0.0001	0.334
8	1.55	0.97	15	4.05	0.96	17	-3.84	0.78	19	0	<0.0001

Table 4. Slopes and correlation coefficients of least-squared regressions of peak strain (μ strain) versus peak force (N) recorded during forward strikes from strain gages attached to the ventral diaphysis of the second metacarpal bone and the dorsal diaphysis of the third and fifth metacarpal bone

Arm	Surface/bone	Buttressed			Unbuttressed			P-value
		Slope	R^2	N	Slope	R^2	N	
3	MC2, ventral	-3.85	0.99	10	-5.52	0.99	11	<0.0001
2	MC5, dorsal	1.16	0.81	14	2.42	0.83	12	0.0034
3	MC3, dorsal	4.03	0.99	12	7.45	0.96	9	<0.0001

phalanges (Maier, 1993; Almécija et al., 2015) whereas *Cebus* has relatively short metacarpals and long phalanges (Jouffroy et al., 1993; Almécija et al., 2015). The short phalanges of *Theropithecus* likely limit the potential for protective buttressing contact of the primary phalangeal pads with the central palm, whereas the long, narrow phalanges of *Cebus* likely limit any significant buttressing contact between primary phalangeal pads and the palmar pads of the proximal phalanges. Additionally, in both *Theropithecus* and *Cebus* the relatively long first metacarpal, compared with the second and third metacarpals, may eliminate any potential for the thenar eminence and thumb to support and wrap around digits 2 and 3 as in a human fist (Morgan and Carrier, 2013). Thus, although the digital length proportions of *Theropithecus* and *Cebus* likely evolved for improved manual dexterity (Almécija et al., 2015), hominins appear to be the only primate group with intra-digit skeletal proportions appropriate for effective buttressing in a fist posture.

In conclusion, protective buttressing of the early hominin hand may be part of a suite of adaptations for intraspecific aggression in australopiths that include the evolution of habitual bipedalism (Carrier, 2011), the retention of short legs for over 2 million years (Carrier, 2007), and protective buttressing of the face (Carrier and Morgan, 2015). Long, thin and highly mobile digits that facilitate delicate and precise manual dexterity are fundamentally incompatible with using the hand as a weapon to strike a rival. Yet, humans are distinguished from the other great apes by both of these behaviors. As suggested previously (Morgan and Carrier,

2013), the evolutionary significance of the proportions of the hominin hand may be that these are the proportions that improved manual dexterity while at the same time making it possible for the hand to be used as a club to threaten and injure opponents.

We wish to emphasize that we are not suggesting that selection on manual dexterity and fighting performance were the only factors that influenced the evolution of hominin hand proportions. There are compelling reasons to suspect that the proportions of the hominin hand were influenced by selection on the foot for terrestrial locomotion (Alba et al., 2003; Rolian et al., 2010). Hand proportions may also have been influenced by other unidentified developmental constraints, as well as other aspects of selection and/or by genetic drift. Given our current understanding of evolutionary processes, it would be naive to suggest that the evolution of a structure with as complex a history as the human hand was influenced solely by one or two components of selection.

MATERIALS AND METHODS

A total of eight male arms, cut at mid-humerus, were purchased from the University of Utah Body Donor Program and from Science Care (Phoenix, AZ, USA). Specimens were not embalmed and were kept frozen until tested. We dissected the forearms to expose the muscles of the wrist and hand. To apply variable tension to the muscle insertion points, high strength fishing line was tied to the tendons distal to the muscles. A 200 lb (where 1 lb \approx 0.45 kg) test line was sutured to the flexor carpi ulnaris and flexor carpi radialis. A 100 lb test line was sutured to the extensor carpi ulnaris and extensor carpi radialis. A 25 lb test line was sutured to the extensor pollicis longus and flexor pollicis longus (thumb abductors), extensor digitorum, flexor digitorum superficialis and flexor digitorum profundus. These last two groups were

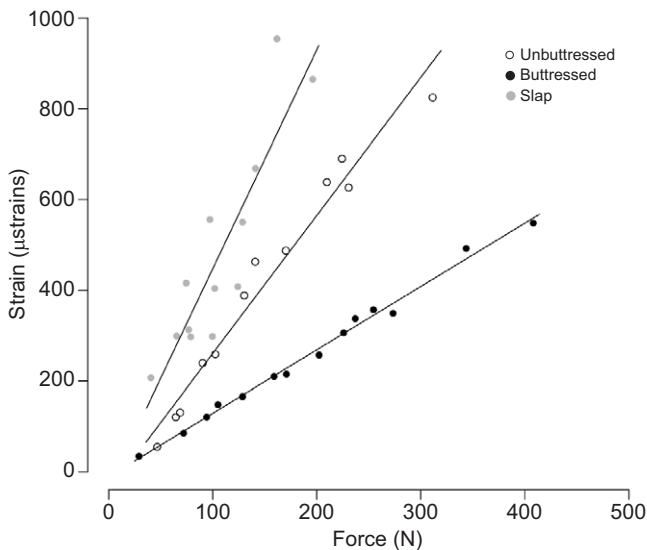


Fig. 2. Relationship of peak strain recorded on the dorsal diaphysis of the second metacarpal versus the peak force during unbuttressed and buttressed forward strikes and slapping strikes. Data are from specimen no. 8. Because slapping strains were compressive (i.e. negative), absolute values of slapping strain are plotted to facilitate comparison with the forward striking data.

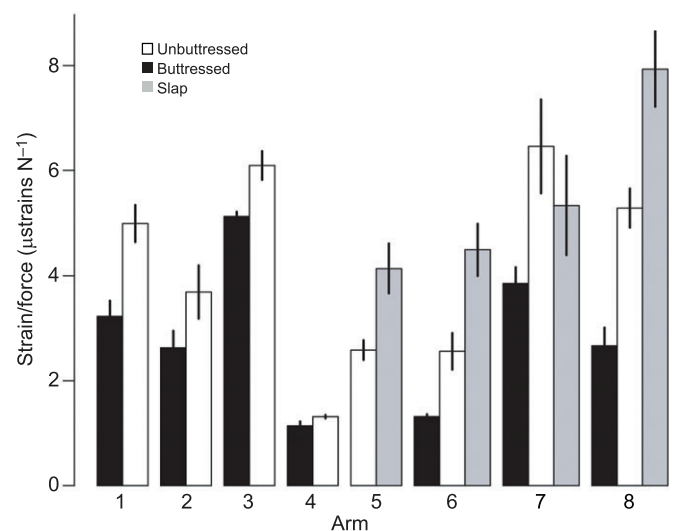


Fig. 3. Means (\pm s.d.) of the ratio of strain versus force for unbuttressed and buttressed forward strikes and slapping strikes for the eight specimens. Because slapping strains were compressive (i.e. negative), absolute values of slapping ratios are plotted to facilitate comparison with the forward striking data.

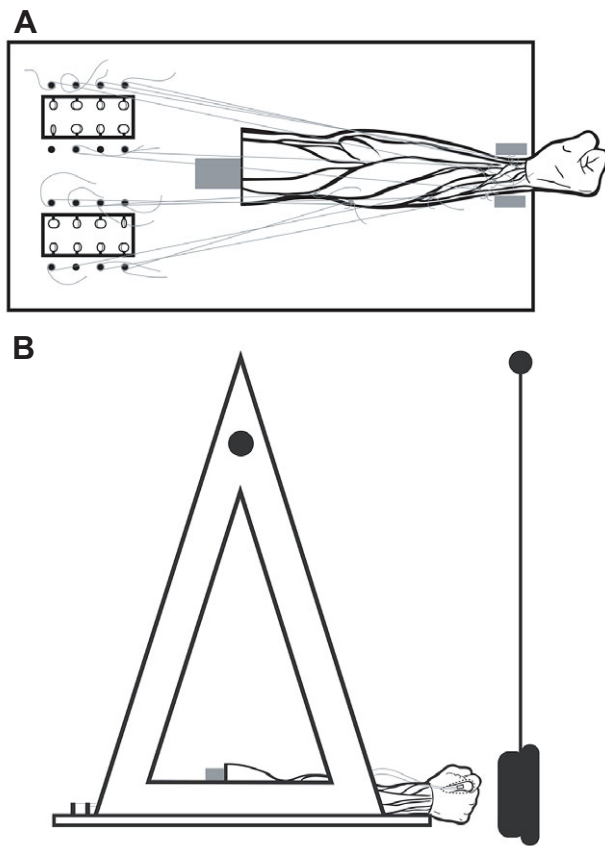


Fig. 4. Illustration of the experimental apparatus used to measure striking strain and force in the metacarpal bones of human cadaver arms. (A) The arm was mounted on a platform with the hand extending beyond the platform. Lines attached to the muscle tendons were secured to guitar tuners at the back of the platform that allowed tension applied to the tendons to be adjusted. (B) The platform was secured in a pendulum what was swung so that the hand struck a mass instrumented with an accelerometer.

separated between digits 2–5 as much as possible depending on the degree of independence of the muscles/tendons. To simulate the thenar adductor muscles of the thumb, which could not be attached to directly without compromising buttressing capabilities, a line was looped around the distal end of the first metacarpal and run perpendicular to digits 2–5 through a redirecting loop around the 5th metacarpal.

Once lines were attached to the muscles, one or more 350 Ω linear foil strain gauges (Micro-Measurements, Raleigh, NC, USA) were attached to the dorsal and/or ventral diaphyses of the palmar metacarpals. A small patch of tissue was cut away from the dorsal side of the second, third or fifth metacarpal, or the ventral side of the second metacarpal to make gauge attachment possible. To verify the orientation of the principle strain during buttressed and unbuttressed forward strikes, a rosette gauge was used to measure strain on the dorsal surface of the second metacarpal in one specimen. Strain was sampled using Micro-Measurement 2120B Signal Conditioning Amplifiers.

Instrumenting the ventral surface of the second metacarpal was relatively destructive, requiring the removal of thenar muscles that were important to the buttressed fist posture. Additionally, gauges placed on the ventral surface of the second metacarpal were susceptible to damage from pressure applied by the second digit during buttressed strikes. For these reasons, although we attempted to record from the ventral surface of the second metacarpal multiple times, we succeeded in getting reliable recordings in only one specimen.

The instrumented arm was mounted on a platform designed to allow the hand to strike an instrumented mass (Fig. 4). The arm was positioned so that the cut diaphysis of the humerus rested against a brace and the hand extended beyond the platform. An additional brace was applied to the dorsal surface of the distal forearm to secure the arm in the direction of striking.

The lines attached to each muscle tendon were tied to guitar tuners mounted on the back of the platform. Turning the tuners varied the tension applied to the tendons, simulating muscle contraction and making it possible to position the wrist and hand in the three striking postures: fully buttressed with the ventral side of the phalanges pressed against the palm and the thumb adducted and flexed to brace the second and third digits; unbuttressed with digits not flexed against the palm and the thumb abducted to provide no buttressing; and an open-palm slap posture with all five digits fully extended. In all of the postures, appropriate tension was applied to the wrist flexor and extensor muscles (i.e. flexor carpi radialis and ulnaris, palmaris longus and extensor carpi ulnaris and radialis) to maintain a stable wrist joint during striking. In the unbuttressed posture, the fingers were flexed at about 100 deg at the metacarpo-phalangeal joints by applying tension to the flexor digitorum superficialis muscle. In the slap posture, in addition to applying significant tension to the wrist flexors and extensors, high levels of tension were applied to all of the flexors and extensors of digits 2–5.

In the fully buttressed posture trials, initial impact with the instrumented mass occurred along the length of the dorsal surface of the proximal phalanx and the distal end of the metacarpal of the instrumented digit (e.g. digit 2). In the unbuttressed posture trials, initial impact with the instrumented mass occurred at the distal end of the metacarpal of the instrumented digit. For slap trials, the fingers were adducted and we adjusted the posture of the hand so that initial impact with the instrumented mass occurred on the ventral (palmer) surface of the head the 2nd metacarpal.

The platform on which the arm was mounted was then secured to a pendulum used to swing the arm so that the hand struck a mass (5.67 kg) instrumented with an Endevco model 7290A-10 Microtron accelerometer (San Juan Capistrano, CA, USA) (Fig. 4B). The system was configured so that the hand struck the instrumented mass at the lowest point of the swing, when the arm's velocity was perpendicular to the vertically oriented striking surface of the mass. The hand impacted the mass at its center and this was padded with 1.5 cm of stiff foam rubber. To insure that the mass responded to the strike by swinging away from the hand rather than spinning, we increased rotational inertia of the mass by placing some of the mass at a distance from the striking point with an aluminium frame. Acceleration of the mass and strain experienced by the metatarsals was recorded at 4000 Hz with a LabView VI.

Reliable recordings depended on realistic formation and alignment of the fist. When setting up the apparatus it was important to ensure that: (1) the hand was positioned so that the instrumented metacarpal was the first to strike the weight, with the others playing little or no role in impact; (2) when switching between buttressed and unbuttressed conformations, the shape of the striking surface of the hand remained unchanged; (3) there was at least some tension in all muscle lines, including muscles not necessary in forming a fist (i.e. extensor digitorum) as activation of these muscles plays an important role in the stability of the wrist and hand; (4) when forming a buttressed fist, digits 2 and 3 were flexed simultaneously with adduction of the thumb as this placed the thenar eminence in a bracing position for these two digits; (5) the digits were fully flexed so that no space remained between the dorsal side of the phalanges and the palm, between any phalangeal bones of any one digit, or between the thumb and digits 2 and 3; and (6) the palm of the hand was aligned with the radius so that little or no flexion or extension of the wrist occurred during striking. One arm was too arthritic to position the hand in the buttressed posture. We were able to collect unbuttressed and slapping, but not buttressed data from this specimen.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

J.H.: design and performance of experiments, data analysis, preparation of manuscript. R.J.: design and performance of experiments. D.R.C.: development of approach, design and performance of experiments, data analysis, preparation of manuscript.

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