

RESEARCH ARTICLE

Sexual dimorphism in human arm power and force: implications for sexual selection on fighting ability

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ABSTRACT

Sexual dimorphism often arises from selection on specific musculoskeletal traits that improve male fighting performance. In humans, one common form of fighting includes using the fists as weapons. Here, we tested the hypothesis that selection on male fighting performance has led to the evolution of sexual dimorphism in the musculoskeletal system that powers striking with a fist. We compared male and female arm cranking power output, using it as a proxy for the power production component of striking with a fist. Using backward arm cranking as an unselected control, our results indicate the presence of pronounced male-biased sexual dimorphism in muscle performance for protracting the arm to propel the fist forward. We also compared overhead pulling force between males and females, to test the alternative hypothesis that sexual dimorphism in the upper body of humans is a result of selection on male overhead throwing ability. We found weaker support for this hypothesis, with less pronounced sexual dimorphism in overhead arm pulling force. The results of this study add to a set of recently identified characters indicating that sexual selection on male aggressive performance has played a role in the evolution of the human musculoskeletal system and the evolution of sexual dimorphism in hominins.

KEY WORDS: Aggression, Human evolution, Fist, Hominidae, Male–male competition, Muscle performance, Primates

INTRODUCTION

In many species, male mating opportunity is determined by fighting ability and performance in male–male contests (Andersson, 1994; Darwin, 1871). This has led to the evolution of male-biased sexual dimorphism in traits that improve fighting performance, such as body mass, weapon size (e.g. canine teeth), and musculoskeletal traits that increase the ability to manipulate or injure opponents (e.g. Clutton-Brock, 1985; Crook, 1972; Morris and Brandt, 2014; Morris and Carrier, 2016; Morris et al., 2019; Plavcan, 2001; Plavcan and van Schaik, 1992, 1997). In many groups of mammals and primates, the degree of dimorphism in fighting-related traits is a general indicator of the intensity of sexual selection on male fighting performance (Clutton-Brock et al., 1977; Mitani et al., 1996; Plavcan, 1999, 2004; Plavcan and Van Schaik, 1997; Puts, 2010, 2016).

The pervasiveness of aggression and violence among male primates has led to the suggestion that these behaviors are general

characteristics of the primate order (Talebi et al., 2009; Wrangham and Peterson, 1996). Within this group, the great apes are also characterized by intense male–male competition (Carrier, 2007; Puts, 2016; Wrangham and Peterson, 1996) and pronounced male-biased sexual dimorphism in traits that improve fighting performance. Fighting among male chimpanzees, which can lead to severe injury and death, involves the use of the forelimbs to grapple, strike and slam an opponent to the ground (Goodall, 1986). Selection on male fighting performance in chimpanzees may be associated with the evolution of sexual dimorphism, with males being 27% larger (Smith and Jungers, 1997) and having broader forearm bones as compared with females (Morris et al., 2019). In gorillas, a more extreme example, fights between males occur in 50% of intergroup encounters (Harcourt, 1978). Male gorilla fighting involves using the forelimbs to strike with the hands and push and pin opponents to the ground (Rosenbaum et al., 2016). Selection on male fighting performance in gorillas may be associated with greater body mass (males are 100% larger than females, on average; Smith and Jungers, 1997), greater forelimb mass (Zihlman and McFarland, 2000) and a larger anatomical mechanical advantage associated with elbow extension, which increases force output during striking (Morris et al., 2019). Similarly, male orangutans, which also fight readily and aggressively (Galdikas, 1979), are 120% larger than females (Smith and Jungers, 1997) and have broader forelimbs that putatively increase striking and grappling performance (Morris et al., 2019).

Similar to other great apes, human males fight frequently and fighting may be highly injurious or lethal (Adams, 1983; Chagnon, 1988; Daly and Wilson, 1988; Keeley, 1996; Puts, 2010; Wrangham and Peterson, 1996). Selection on male fighting performance in humans has led to similar sexual dimorphism to that in other great apes: males have 41% greater fat-free body mass, 75% more muscle mass in the arms and, consequently, 90% greater upper body strength than females (as compared with 50% more muscle mass and 65% more muscle strength in the legs; Lassek and Gaulin, 2009). The large degree of sexual dimorphism in the upper bodies of humans may be a result of sexual selection on males for improved performance during male–male competition (Carrier, 2011; Lassek and Gaulin, 2009; Morgan and Carrier, 2013; Puts, 2010).

Recently, Morgan and Carrier (2013) and Horns et al. (2015) have shown that the unique ability of humans to form a fist decreases the likelihood of hand injuries during striking, thereby allowing a greater ability to use the fist to transmit large striking forces to an opponent. Results consistent with this ‘protective buttressing hypothesis’ may reflect sexual selection on hand morphology and the importance of striking with a fist in male–male contests (Morgan and Carrier, 2013). Striking with a fist is common when humans fight and a hand clenched into a fist is often used as a threat display, indicating its likely importance as a weapon (Enquist, 1985; Maynard Smith and Price, 1973; Parker, 1974; Szalai and Számadó, 2009; Számadó, 2008). Similarly, the muscles that propel the fist are

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likely important for fighting performance. Given that sexual dimorphism is often most pronounced in traits that improve fighting performance in other mammalian species, we expected to find that muscle performance important for striking with the fist will be sexually dimorphic in humans.

Here, we tested for the presence of sexual dimorphism in muscular action that powers striking with a fist. We used single-arm forward arm cranking (shoulder flexion and elbow extension) as a proxy for striking with a fist. This method is advantageous for several reasons. Arm cranking has a lower likelihood of injury than punching and, because of this, it allows maximum effort from subjects that have no training in striking technique. This allowed us to sample from a broader population, given that training was not a prerequisite. Indeed, we excluded those with any training in martial arts in order to get a more representative sample of the general population. Both forward cranking and punching require active forward, horizontal flexion of the arm at the shoulder joint by the anterior deltoid and pectoralis muscles and extension of the elbow by the triceps muscle. Previous research on arm cranking using electromyography (EMG) indicates high levels of recruitment of the anterior deltoid, pectoralis and triceps brachii during forward but not reverse arm cranking, whereas the infraspinatus, posterior deltoid and biceps brachii (a primary elbow flexor and antagonist to the triceps) exhibit high activity levels during reverse but not forward arm cranking (Bressel and Heise, 2004; Kumar, 1986; Smith et al., 2008). Similar to these results, EMG during forward punching indicates high levels of muscle recruitment in the pectoralis and triceps brachii with lower recruitment levels in the infraspinatus and little contribution from the biceps brachii (Kimura et al., 2007; Vences Brito et al., 2011), providing sufficient similarities in muscle recruitment patterns for using forward arm cranking as a proxy for striking with a fist. This method allows comparison of the level of sexual dimorphism in forward (shoulder flexion and elbow extension) versus backward (shoulder extension and elbow flexion) arm cranking power. The hypothesis that males are more anatomically specialized for forward punching led us to predict that greater sexual dimorphism will exist in forward than in backward arm cranking.

Finally, to test an alternative hypothesis that sexual dimorphism in arm muscle performance evolved as a result of selection on male overhead throwing ability (Lombardo and Deaner, 2018a,b), we collected data on single-arm overhead forward and backward static pulling force. We compared male and female forward overhead pulling force using a similar approach (using backward overhead pulling force as a control) and compared these results with those of the arm cranking trials in an attempt to understand which, if either, might have been a stronger selective force on arm muscle performance in humans.

MATERIALS AND METHODS

Subjects

We collected data from 19 women and 20 men aged 21–35 years (mean 28.7 ± 3.9 years). Participants were assessed for physical fitness using the International Physical Activity Questionnaire ('usual week' version; Craig et al., 2003). To participate in the study, subjects had to score a 2 (moderate physical activity) or 3 (high physical activity) on the survey and had to be right-hand dominant. Subjects were also screened for injuries and muscular or neurological disorders. Furthermore, to limit possible bias in performance, we did not include subjects who responded that they lift weights more than three times per week, participated in body building, or trained regularly in martial arts. Subjects gave informed

consent and all procedures were approved by the University of Utah Internal Review Board (Approval # IRB_00073779).

Anthropometry

For each subject, we collected the following information: age (years), height (m), mass (kg), length and circumference of the upper arm, forearm and hand, and a skin-fold measurement from the back of the upper arm (triceps brachii), in accordance with the Anthropometric Standardization Reference Manual (Lohman et al., 1988). All arm metrics were measured on the arm used in data collection trials (i.e. the dominant arm). From the anthropometric data, we calculated upper arm fat-free cross-sectional areas (ffCSA; Inglis et al., 2013).

Experimental set-up and protocol

Seated arm-cranking trials were performed on a custom-built inertial load ergometer modified to measure power during arm cranking (modified from Martin et al., 1997; Fig. 1). The ergometer frame was mounted to a platform on which a custom-built chair was rigidly mounted. The crank arm was attached to a flywheel (inertia = 0.0783 kg m^2) via a 44-tooth chainring with a 25-tooth gear drive and an internal gear ratio of 8:1. Flywheel angular velocity and acceleration were measured using an optical sensor mounted on the ergometer frame. The sensor measured the movement of a slotted disk, with three slots separate by 90 deg, mounted on the flywheel. The overall gear ratio (28.16:1) resulted in data acquisition occurring every 3 deg of crank arm rotation. This allowed power to be calculated instantaneously (P_{inst} , in W) every 3 deg of arm crank rotation, using the following formula:

$$P_{\text{inst}} = I_{\text{flywheel}} \times \alpha_{\text{flywheel}} \times \omega_{\text{flywheel}}, \quad (1)$$

where I_{flywheel} is the moment of inertia of the flywheel, α_{flywheel} is the angular acceleration of the flywheel and ω_{flywheel} is the angular velocity of the flywheel, with both angular acceleration and angular

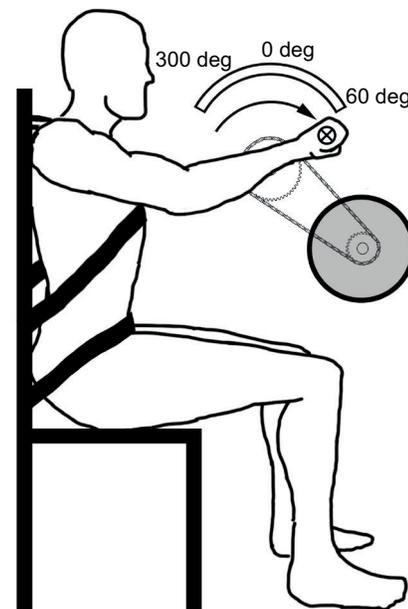


Fig. 1. Illustration of the arm crank apparatus. The arrow indicates the path of movement of the handgrip for a forward arm cranking stroke. The gray shaded circle is the flywheel. Structural details have been omitted for clarity. Drawing adapted from Bressel and Heise (2004).

velocity calculated from the measured velocity data (Martin et al., 1997). Mean power (P_{mean}) was calculated as the average of all P_{inst} values for one forward or backward stroke of the crank arm.

For each subject, the mounted chair was adjusted vertically such that the subject's arm motion was in the horizontal plane with the handgrip starting at the height of the acromion process; the chair was positioned horizontally such that a subject's arm was limited to 90% of full elbow extension in order to minimize the possibility of injury. A seat-belt and two shoulder straps were tightened across the torso to limit the contribution of the torso muscles to accelerating the crank arm. The handgrip was perpendicular to the crank arm and all trials were conducted with the hand gripping in a pronated position. The non-dominant arm rested in the lap. Both forward and backward arm cranking trials were completed using the same set-up. Subjects completed a 3 min warm-up of low-intensity arm cranking followed by a 1 min rest period prior to data collection. Each subject completed three trials in both the forward and backward cranking direction. Each trial began with the crank arm at rest and flywheel at zero velocity. A single cranking consisted of maximal acceleration for a third of a crank turn: from 300 deg, through 0 deg, to 60 deg, where 0 deg is top dead center, for a forward cranking trial, and through the reverse path for a backward cranking trial (Fig. 1). Each trial consisted of 7 forward or backward accelerating strokes, occurring in approximately 3–4 s, with the subject effortlessly reversing the crank arm to the starting position after each stroke. Subjects were given a countdown and were vocally encouraged to maximally accelerate the crank arm through the entire range of motion. Rest periods of 1 min were performed between trials.

For the overhead pulling trials, we tried many configurations of the arm-crank set-up in attempt to collect power data comparable to the first set of arm-cranking trials. However, the peculiar motion of overhead arm cranking causes challenges for subjects: many stated that the awkwardness of the motion did not allow them to maximize their performance and that the movement seemed to test motor coordination more than muscle performance. Because of this constraint, we instead used static overhead pulling because it is a natural motion (similar to overhead throwing) and allowed subjects to maximize their performance. This set-up resulted in the collection of force data as opposed to power data. For these trials, the chair set-up was similar and was attached to a rigid platform (Fig. 2). A grip was attached to a wire cable, which was attached in series to a force transducer (AmCells STL Series S-Type Alloy Steel Load Cell, Tacuna Systems, Golden, CO, USA), which was anchored to a brick wall. For each subject, the chair was adjusted horizontally such that, when pulling, the subject's hand was positioned directly above the shoulder but over the head, with the elbow bent to 90 deg; the chair was positioned vertically such that, when pulling, the wire cable was horizontal. The grip was attached so that the hand gripped in a 'power grip' position (palm facing inward, thumb pointing upward). The non-dominant arm rested in the lap. Both forward and backward overhead pulling trials were completed using the same set-up; the chair faced away from the wall for forward pulling and toward the wall for backward pulling. Subjects completed several practice pulls at low intensity to familiarize themselves with the action. Three forward pulls and three backward pulls were completed by each subject, with a 1 min rest between trials. Voltages from the force transducer were amplified (AC/DC amplifier model P122, Grass Instruments, Quincy, MA, USA), collected at 5 Hz using a Biopac MP100 (Biopac Systems, Inc., Goleta, CA, USA), and converted into units of force (in N). Weights of 5, 10 and 25 pounds (where 1 lb \approx 0.45 kg) were used for calibration.

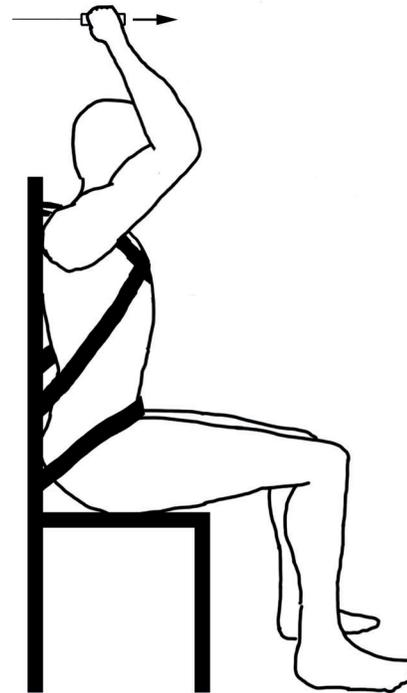


Fig. 2. Illustration of the overhead pulling apparatus. The arrow indicates the path of movement of the handgrip for a forward overhead pull. The wire attached to the handgrip was connected to a force transducer (not shown). Structural details have been omitted for clarity.

Statistical analysis

All data were ln-transformed prior to analysis. All data were normally distributed ($P>0.05$; Shapiro–Wilk tests) with similar variances between groups ($P>0.05$; Bartlett's tests). For each subject, the single best forward and backward arm cranking strokes (achieving the highest P_{inst} or highest P_{mean}) out of 7 total strokes for each trial were used for analysis. For overhead pulling trials, the single best forward and backward overhead pulls (achieving the highest force) were used for analysis. To control for overall strength differences between males and females, we used a ratio of forward values divided by backward (control) values for each subject. We analyzed raw data and forward/backward ratios using t -tests and analysis of covariance (ANCOVA) with body mass (in kg) and upper arm ffCSA (in mm²) as covariates. Within-test P -values were adjusted to correct for multiple comparisons using the false discovery rate procedure (Benjamini and Hochberg, 1995). Significance levels were set at $\alpha=0.05$ and all tests were two-tailed. All analyses were carried out in R (version 3.5.2; <http://www.R-project.org/>).

RESULTS

Males achieved greater values for forward and backward P_{mean} , ratio of forward/backward P_{mean} , forward and backward P_{inst} , and forward overhead pulling force, as indicated by significant results ($P<0.05$) for both t -tests and ANCOVA (Tables 1 and 2, Figs 3 and 4). A male-biased difference in the ratio of forward/backward P_{inst} was significant when comparing values using a t -test ($P<0.05$) but not when using body mass or upper arm ffCSA as covariates (ANCOVA, $P=0.354$ and $P=0.221$, respectively; Table 2). For backward overhead pulling force, we also found mixed results, with a t -test indicating a significant male-biased difference ($P<0.05$) but no significant differences using ANCOVA tests with body mass or

Table 1. Descriptive statistics for arm cranking and overhead pulling trials

Trial	Female	Male	Males greater by (%)
P_{mean} (W)			
Forward	107.58±26.33	281.62±65.08	162
Backward	143.95±27.66	295.40±54.89	105
Forward/backward	0.75±0.11	0.96±0.13	28
P_{inst} (W)			
Forward	168.93±46.32	431.43±96.09	155
Backward	218.54±42.37	480.20±103.65	120
Forward/backward	0.76±0.11	0.91±0.13	20
Overhead pulling force (N)			
Forward	505.17±109.26	1113.82±285.91	120
Backward	275.01±119.53	487.25±136.35	77
Forward/backward	2.02±0.62	2.40±0.66	19

P_{mean} , mean arm cranking power; P_{inst} , instantaneous arm cranking power. Data are means±s.d. and the percent difference for males versus females is shown.

upper arm ffCSA as covariates ($P=0.109$ and $P=0.141$, respectively; Table 2). For the ratio of forward/backward overhead pulling force, no significant differences were found ($P>0.05$ in all tests). ANCOVA results indicated significant effects ($P<0.05$) of anthropometric covariates (body mass or upper arm ffCSA) in all tests except for forward/backward overhead pulling force (Table 2). No significant interaction terms were present in any ANCOVA test ($P>0.05$ for all). The degree of sexual dimorphism in forward, backward and forward/backward P_{mean} was greater for arm cranking (males greater by 162%, 105% and 28%, respectively) than for P_{inst} (males greater by 155%, 120% and 20%) and overhead pulling (120%, 77% and 19%; Table 1). Anthropometric, arm cranking and overhead pulling trial data used in the analysis are available in Table S1.

DISCUSSION

Our results indicated that there is greater sexual dimorphism in forward than in backward arm cranking power and that males have a greater ratio of forward to backward arm cranking power than

Table 2. Comparison of female and male data from arm cranking and overhead pulling trials

Trial	t-test		ANCOVA			
	t	P	Body mass covariate		ffCSA covariate	
			F	P	F	P
P_{mean} (W)						
Forward	-12.90	<0.001	26.31	<0.001 [‡]	24.03	<0.001 [‡]
Backward	-11.76	<0.001	19.23	<0.001 [‡]	15.67	<0.001 [‡]
Forward/backward	-5.30	<0.001	5.48	0.025 [‡]	6.50	0.015 [‡]
P_{inst} (W)						
Forward	-11.81	<0.001	18.76	<0.001 [‡]	17.29	<0.001 [‡]
Backward	-11.55	<0.001	18.70	<0.001 [‡]	15.58	<0.001 [‡]
Forward/backward	-3.61	<0.001	0.88	0.354 [‡]	1.55	0.221 [‡]
Overhead pulling force (N)						
Forward	-10.80	<0.001	21.93	<0.001 [‡]	16.43	<0.001 [‡]
Backward	-5.71	<0.001	2.90	0.109 [‡]	2.96	0.141 [‡]
Forward/backward	-1.82	0.077	2.69	0.109	0.92	0.344

P_{mean} , mean arm cranking power; P_{inst} , instantaneous arm cranking power; ffCSA, fat-free cross-sectional area. ANCOVA results are shown with body mass or ffCSA as covariate.

[‡]Significant effect of body mass or upper arm ffCSA covariate ($P<0.05$). No significant interactions in any ANCOVA test were found.

All P -values were corrected for multiple comparisons using the false discovery rate procedure. Significant P -values (<0.05) are in bold.

females. These results suggest that sexual selection has occurred on muscle performance associated with shoulder flexion and elbow extension power. This is consistent with the hypothesis that male-biased sexual dimorphism in upper body strength is driven, in part, by selection on performance in punching with a fist. Our data provide less support for the hypothesis that selection on overhead throwing ability is the cause of male-biased sexual dimorphism in upper body strength (Lombardo and Deaner, 2018a,b). Less sexual dimorphism was observed in overhead pulling force and no statistically significant dimorphism was found in the forward/

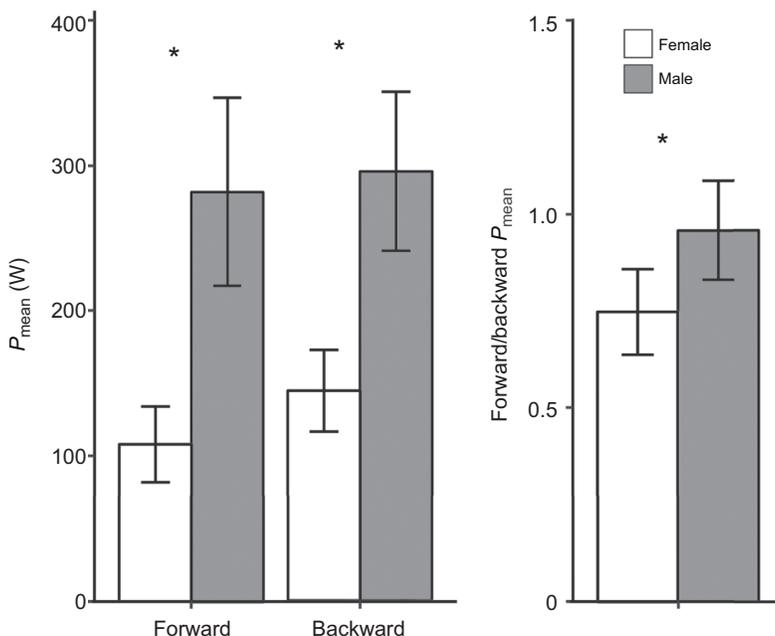


Fig. 3. Summary of mean arm cranking power (P_{mean}). Males ($n=20$) had greater P_{mean} than females ($n=19$) for both forward and backward cranking and for the ratio of forward to backward P_{mean} ($*P<0.05$, t -tests and ANCOVA). Error bars represent ± 1 s.d.

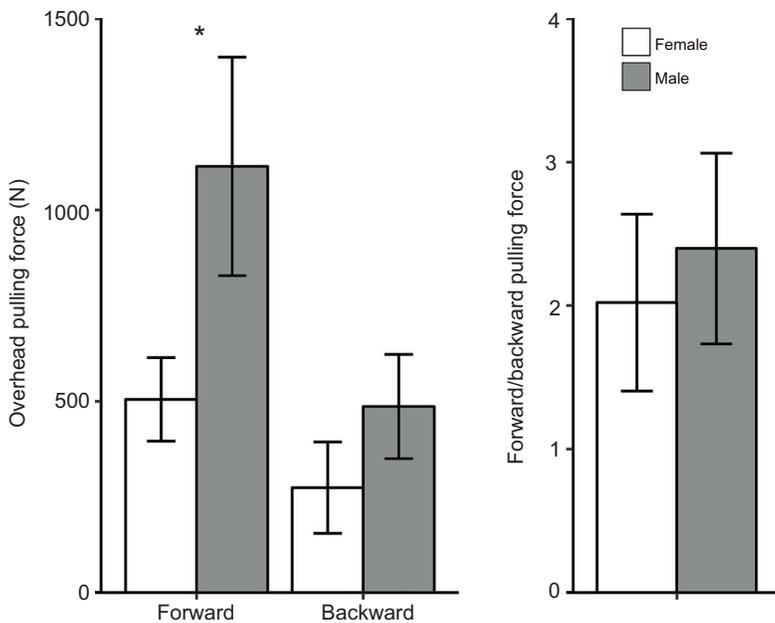


Fig. 4. Summary of data from overhead pulling trials. Males ($n=20$) had greater mean force output than females ($n=19$) for forward overhead pulling trials; inconsistent results were found for backward overhead pulling, and no significant differences were found for the ratio of forward to backward force ($*P<0.05$, t -tests and ANCOVA). Error bars represent ± 1 s.d.

backward overhead pulling force ratio. Together, these observations suggest that the motion of powerful shoulder flexion and elbow extension, the actions that power punching with a fist, has undergone greater positive selection in males than in females.

Our results are consistent with previous data indicating high levels of sexual dimorphism in upper body muscle performance and associated musculoskeletal traits. Specifically, data from Bohannon (1997) show a greater degree of male-biased sexual dimorphism in elbow extension (males 101% greater in absolute muscle force and 56% greater in force per unit body mass) than in elbow flexion (76% and 37% greater, respectively) in subjects aged 20–39 years. Males have 75–78% more muscle mass in the arms, as compared with 41–50% more muscle mass in the legs, than females (with total body muscle mass being 45% greater in males; Lassek and Gaulin, 2009; Nindl et al., 2002). In terms of skeletal mass, males also have 20–25% greater bone mineral content in the bones of the forelimbs, a trait required for larger muscle attachment areas and greater ability to withstand larger forces produced by larger muscles. Interestingly, male-biased sexual dimorphism in forelimb skeletal robusticity has also been identified in australopiths (McHenry, 1986, 1991, 1996), suggesting that sexual dimorphism in muscular mass and muscle performance traits in the forelimbs has a long evolutionary history in hominins (see also Morgan and Carrier, 2013).

Our results are consistent with numerous other studies showing the connection between the intensity of male–male aggression, anatomical specialization for fighting, and sexual dimorphism in specific traits associated with fighting performance. For example, both carnivores and primates fight using their teeth, jaws and forelimbs as primary weapons during aggressive encounters. Male-biased sexual dimorphism in canine size, muscle moment arms in the jaw-closing muscles, and skeletal traits associated with increased muscle mass and force output is found in these groups and is greatest in species with high levels of male–male competition (Gittleman and Van Valkenburgh, 1997; Kay et al., 1988; Leutenegger and Kelly, 1977; Morris and Carrier, 2016; Morris et al., 2019; Plavcan, 2001; Plavcan and van Schaik, 1992; Thorén et al., 2006). An example more comparable to the way that humans fight comes from another biped, the kangaroo. Male kangaroos fight aggressively for dominance status and access to females. When

fighting, males stand on their hindlimbs (and tail) and use their forelimbs to grapple, push and strike their opponent. Selection on fighting ability has led to the evolution of male-biased sexual dimorphism in forearm length and muscle mass in the forearms, chest and shoulders (Jarman, 1983, 1989; Warburton et al., 2013). Thus, for a weapon to be used effectively, the musculoskeletal structures underlying its use must also be specialized. In humans, in which males frequently fight and injure each other, specialization for arm protraction accompanies use of the fist as a primary weapon. These results are consistent with a growing body of evidence suggesting that specialization for male fighting has played a role in the evolution of the musculoskeletal system of humans. For example, the robust skull, short limbs, plantigrade foot posture and bipedal posture of hominins may also be associated with improved aggressive performance (Carrier, 2007, 2011; Carrier and Cunningham, 2017; Carrier and Morgan, 2015).

Our data on overhead pulling suggest that overhead throwing may not be as strong a selective agent on shoulder flexion and elbow extension muscle performance as striking with a fist (using arm cranking as a proxy). However, given that there are some similarities in muscles recruited for these two actions (Illyés and Kiss, 2007), it is possible that selection on one could improve performance in the other. One related caveat of this study is that we measured power and force outputs from muscle action only. Recent evidence has shown that overhead throwing involves elastic energy, stored in tendons and ligaments of the shoulder during the arm-cocking phase, and released during elbow extension to contribute up to half of the force of throwing an object (Roach et al., 2013). It is possible that selection on overhead throwing acted on mechanisms of elastic energy storage and recovery, which may explain the smaller degree of dimorphism in muscle-only forward overhead pulling found in our study. Additionally, most of the work produced for an overhead throw is generated in the hips and torso; active elbow extension contributes little to the total work produced (reviewed in Roach and Lieberman, 2014), suggesting that selection on elbow extension power to improve overhead throwing performance may be weak.

Archaeological evidence suggests that the hand proportions required to make a buttressed fist, which likely aligns with its earliest use as an effective weapon, were present in early hominins

and may have first appeared at approximately the same time as habitual bipedalism (reviewed in Morgan and Carrier, 2013). This is well before adaptations for overhead throwing arose in hominins, which are suggested to have first appeared in *Homo erectus* (Roach et al., 2013) or later *Homo* species (Larson, 2007; Lombardo and Deaner, 2018a). Specialization for striking with a fist indeed may have served as a preadaptation for improved overhead throwing that developed later in hominin history. Future studies measuring elastic force contribution to punching force and comparative evolutionary studies of the hominin shoulder in these contexts may help to resolve this.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: J.S.M.; Methodology: J.S.M., J.L., J.C.M., D.R.C.; Software: J.S.M., J.L., J.C.M.; Validation: J.L., J.C.M.; Formal analysis: J.S.M., J.L.; Investigation: J.S.M.; Resources: J.S.M., J.C.M.; Data curation: J.S.M., J.L.; Writing - original draft: J.S.M.; Writing - review & editing: J.S.M., J.L., J.C.M., D.R.C.; Visualization: J.S.M.; Supervision: J.S.M.; Project administration: J.S.M., J.L.; Funding acquisition: J.S.M., D.R.C.

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Supplementary information

Supplementary information available online at

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