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RESEARCH ARTICLE

Straight arm walking, bent arm running: gait-specific elbow angles

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ABSTRACT

Stereotypically, walking and running gaits in humans exhibit different arm swing behavior: during walking, the arm is kept mostly straight, while during running, the arm is bent at the elbow. The mechanism for this behavioral difference has not been explored before. We hypothesized that a mechanical tradeoff exists between the shoulder joint and the elbow joint. Bending the elbow reduces the radius of gyration of the arm and reduces shoulder muscle torque, but at the price of increasing elbow torque. We predicted that the mechanical tradeoff would result in energetics that favored straight arms during walking and bent arms during running. The hypothesis was tested experimentally by having eight subjects walk and run with both straight arms and bent arms while recording arm swing mechanics, and oxygen consumption in a subset of six subjects. The mechanical tradeoff hypothesis was confirmed, with bent arms reducing normalized shoulder muscle torque in both gaits (walking: −33%, running: −32%) and increasing normalized elbow muscle torque in both gaits (walking: +110%, running: +30%). Bent arms increased oxygen consumption by 11% when walking, supporting our prediction that energetics favor straight arms during walking. However, oxygen consumption was equivalent for the straight and bent arm running conditions, and did not support our running prediction. We conclude that straight arms are stereotyped in walking as a result of optimal energetics, while the mechanism leading to bent arms during running remains unknown.

KEY WORDS: Arm swing, Locomotion, Biomechanics, Gait

INTRODUCTION

Although humans swing their arms during both walking and running, elbow angle typically differs between the gaits. Walkers use a 'straight arm', with the elbow close to full extension. Runners use a 'bent arm', with the elbow flexed and the forearm close to perpendicular with the upper arm. Surprisingly, the reason for this difference has been poorly studied. Intuitively, bending the arm when running shortens its length, thus reducing the rotational inertia, making it easier and less costly to swing, especially during running when swing frequency is rapid and muscle torques produced at the shoulder are large. However, reducing the effective length of the arm should benefit both walking and running, so a gait-specific mechanism for the difference must exist beyond simply reducing rotational inertia of the entire arm.

Why humans swing their arms during locomotion has been well established: the reciprocal motions of contralateral arm–leg pairs

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balance angular momentum about the vertical axis internally by transferring momentum between the limbs via the trunk (Bruijn et al., 2008; Collins et al., 2009; Elftman, 1939; Herr and Popovic, 2008). Internal momentum balance reduces the need for an external ground reaction torque at the foot, which is likely to be metabolically costly (Collins et al., 2009; Li et al., 2001; Umberger, 2008). How humans swing their arms is less well established despite much research. Arm swing can be described as a pendulum operating under a combination of passive and active dynamics (Canton and MacLellan, 2018; Collins et al., 2009; Elftman, 1939; Goudriaan et al., 2014; Kubo et al., 2004; Kuhtz-Buschbeck and Jing, 2012; Meyns et al., 2013). Gravitational torque is a major component of arm swing, as are external driving accelerations that transfer energy from the legs to the arms via the trunk (Collins et al., 2009; Kubo et al., 2004; Pontzer et al., 2009). At the same time, active muscle recruitment develops torques in the trunk, shoulder and elbow joints (Ballesteros et al., 1965; Canton and MacLellan, 2018; Collins et al., 2009; Elftman, 1939; Kuhtz-Buschbeck and Jing, 2012). Neuromuscular control of arm swing is rooted in the central patterns of human gait (Barthelemy and Nielsen, 2010; Cappellini et al., 2006; Dietz et al., 2001), and may be conserved from quadrupedal ancestry (Dietz, 2002).

Arm swing occurs mainly in the parasagittal plane, yet is linked to angular momentum about the vertical axis. The linkage is partly accomplished by the horizontal joint reaction force at the shoulder (JRF_H) that arises from swing. JRF_H causes a transverse plane reaction torque (τ_{trv}) on the thorax (Fig. 1A), which is further linked to the lower body by trunk torsion to transfer momentum between the upper and lower limbs. In the arm, muscle torques occur at the shoulder (τ_{sho}) and the elbow (τ_{elb}), generally opposing angular excursion and acting in a resistive manner (Collins et al., 2009) (Fig. 1A). τ_{sho} is most simply explained as resembling a rotational spring and acting on a functionally rigid single pendulum arm. Bending the elbow moves the center of mass (CoM) of the pendulum closer to the shoulder pivot, reducing the radius of gyration (R_G) and the required τ_{sho} (Fig. 1B).

In order to maintain functional approximation of a single pendulum arm, τ_{elb} must resist external forces that would cause an external torque at the elbow and rotation of the forearm relative to the upper arm. Gravity is one such external force. Pseudoforces from acceleration of the thorax also place external torques on the forearm in the reference frame of the upper arm. Vertical acceleration measured at the shoulder has a much higher magnitude compared with horizontal acceleration in walking (Kubo et al., 2004). Similarly, measurements of linear displacements at the C7 vertebral level indicate larger vertical than horizontal accelerations in both walking and running (Thorstensson et al., 1984). Other forces causing external elbow torques arise from centripetal and tangential accelerations of the elbow joint center in the arm reference frame. The net effect of all these forces is likely a large vertical external force component contributing to the external elbow torque, and a smaller horizontal component. Bending the elbow to reduce arm R_G brings the forearm closer to horizontal, thus
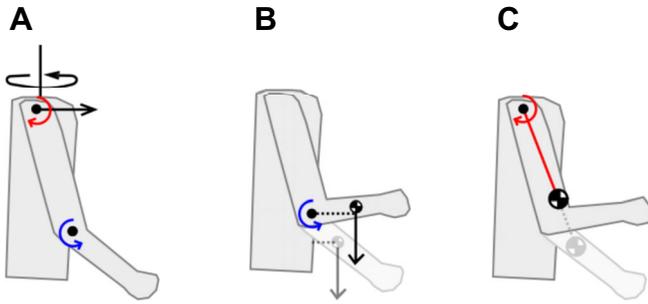
Fig. 1. Illustration of the mechanical tradeoff hypothesis. (A) Three relevant torques (curved arrows) occur during arm swing: muscle torque at the elbow (τ_{elb}), muscle torque at the shoulder (τ_{sho}) and transverse reaction torque on the thorax (τ_{trv}) arising from the horizontal joint reaction force at the shoulder (JRF_H, straight arrow). (B) When the arm is bent at the elbow, the center of mass of the arm moves closer to the shoulder joint, reducing rotational inertia of the arm and the burden on the shoulder muscles. (C) At the same time, the moment arm (dashed line) for vertical external forces acting on the forearm increases with the bent arm, increasing the burden on the elbow muscles.

increasing the moment arm of the net vertical external force (Fig. 1C). Conversely, maintaining a straight arm places the forearm more parallel with the vertical forces, limiting the external torque they produce and consequently the resistive τ_{elb}.

We propose a mechanical tradeoff hypothesis that posits a tradeoff between muscle torques at the shoulder and the elbow linked to the average elbow angle. Flexing the elbow, thus shortening the arm's moment of inertia, reduces the shoulder muscle torque but at the cost of increasing the elbow muscle torque. We predict that the energetic consequences of the mechanical tradeoff favor straight arm walking and bent arm running, and that elbow angle is determined by energetic cost for each gait. Studies show that perturbation of normal arm swing, typically by holding or binding the arms to the torso, increases the net energy cost of locomotion by up to ~10% in both walking (Collins et al., 2009; Ortega et al., 2008; Umberger, 2008) and running (Arellano and Kram, 2014; Egbuonu et al., 1990; Tseh et al., 2008), indicating that normal arm swing is an important cost-saving mechanism. We also predict similar non-trivial energy costs to altering normal elbow angle. We tested our hypothesis and predictions by conducting an experiment with human subjects who walked and ran with both flexed and extended elbows.

MATERIALS AND METHODS
Eight healthy subjects (four males and four females, age 26.6±2.5 years, mass 76.6±15.9 kg, mean±s.d.) participated in the experiment. Prior approval was granted by the Harvard University Institutional Review Board, and all subjects gave informed consent. Subjects walked and ran on a split-belt treadmill instrumented with force plates (Bertec Corp., Columbus, OH, USA). Four randomized experimental conditions were conducted in random order: straight arm walking (SW), bent arm walking (BW), straight arm running (SR) and bent arm running (BR). For SW and BR, the subjects were asked to walk and run normally. For BW, subjects were instructed to hold their forearm as they would during running; similarly, the instruction for SR was to hold the forearm as they would during walking. All walking trials were done at a single dimensionless speed (Fr number Fr=0.2, range: 1.30 to 1.44 m s^{-1}), and running trials were also done at a single dimensionless speed (Fr=1, range: 2.90 to 3.22 m s^{-1}). Each condition lasted 3 min, with data collection occurring during the last minute. Six subjects returned

within 2 weeks for energetic data collection (see below). All analyses used the Igor Pro software platform (Wavemetrics, Lake Oswega, OR, USA).

Kinematic and kinetic time series
Motions of the right forearm, right upper arm and thorax were captured with eight infrared cameras recording at 200 Hz (Qualysis Motion Capture Systems, Gothenburg, Sweden). Reflective markers were placed on the left and right acromia, right humeral epicondyles, and right radial and ulnar styloid processes. The right shoulder joint was estimated to be 3.0 cm (females) or 3.5 cm (males) below the right acromion marker (De Leva, 1996). The elbow joint center was calculated as the midpoint between the humeral epicondyles, and the wrist joint center was calculated as the midpoint between the styloid processes. The radius of the thorax was estimated as half the distance between the left and right acromia. Raw time series were filtered using a 10 Hz low-pass filter.

Analyses were done on the right arm segments in a parasagittal plane. Shoulder angle (θ_{sho}, rad) was defined as the angle formed by the upper arm and the vertical. Elbow angle (θ_{elb}, rad) was defined as the angle formed by the forearm and upper arm, with a straight arm being the neutral position. Angles followed the right hand rule, with positive angles representing flexion. Segmental inertias for the forearm and upper arm were estimated using subject metrics and anthropometric tables (De Leva, 1996). Standard inverse dynamics equations were used to calculate joint reaction forces, τ_{sho} (N m) and τ_{elb} (N m) (Winter, 2009). JRF_H (N) was multiplied by the radius of the thorax (m) to yield τ_{trv} (N m). Right heel strikes were used to define strides, and were determined from the vertical force traces under the right foot. Ten consecutive strides were averaged for each subject and condition. Inter-subject stride averages and s.e.m. were then calculated.

Kinetic variables were extracted from the individual stride averages. The magnitude of each torque ($\Delta\tau_{trv}$, $\Delta\tau_{sho}$ and $\Delta\tau_{elb}$) was calculated as the difference between the maximum and minimum values across the stride. $\Delta\tau_{sho}$ and $\Delta\tau_{elb}$ were normalized to dimensionless muscle torques ΔT_{sho} and ΔT_{elb} by dividing by $\Delta\tau_{trv}$. Inter-subject means and s.e.m. were calculated for each variable. We normalized by transverse torque because it represents the mechanical link between arm swing in the sagittal plane and angular momentum about the vertical axis, and can be thought of as the relevant output of sagittal plane arm swing. We prefer normalizing by a functional measure rather than standard size dimensions (Hof, 1996) because the method controls for inter-subject variation in the contribution of arm swing to total angular momentum dynamics.

Energetics data collection
Following the initial experiment, six of the original subjects returned within 2 weeks and repeated the experiment while we collected metabolic data. Energetics were obtained from oxygen consumption, measured using an open-flow respirometry system (Sable Systems, North Las Vegas, NV, USA) and standard equations (Withers, 1977).

Resting oxygen consumption was recorded first, with the subject standing quietly on the treadmill. The four experimental conditions followed in a randomized order. Each condition, including rest, lasted for 5 min. Average oxygen consumption across the last 2 min was extracted to represent steady-state energetics. Oxygen consumption rates were normalized using body mass, and resting metabolism was subtracted from the walking and running conditions to calculate net oxygen consumption, $\dot{V}_{O_2,net}$ (ml O$_2$ min^{-1} kg^{-1}).
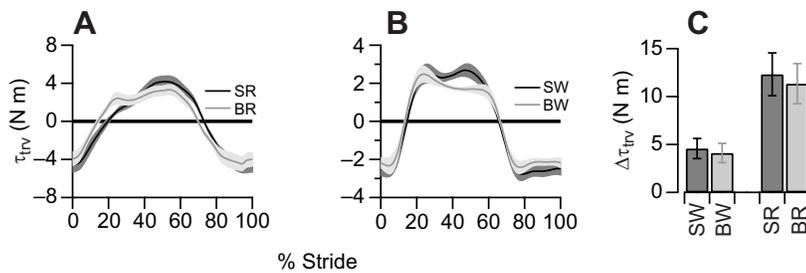
Fig. 2. Comparison of transverse reaction torques (τ_{trv}) between experimental conditions. (A,B) Inter-subject averages across the stride for (A) walking and (B) running. Shaded bands are ±1 s.e.m. (C) Magnitude of transverse reaction torques across the stride. Error bars are ±1 s.e.m. SR/SW, straight arm running/walking; BR/BW, bent arm running/walking.

Statistics

Comparisons between experimental condition means were done for walking and running separately: SW versus BW and SR versus BR. Repeated measures ANOVA (threshold $P=0.05$) was used to assess statistical differences between mean values for $\Delta\tau_{trv}$, $\Delta\mathbf{T}_{sho}$, $\Delta\mathbf{T}_{elb}$ and $\dot{V}_{O_2,net}$.

RESULTS
Transverse reaction torque

In all four conditions, τ_{trv} showed a consistent pattern of peak clockwise torque near ipsilateral heel strike and peak counter-clockwise torque near contralateral heel strike (Fig. 2A,B), with both occurring mainly at stride frequency. Comparison between the magnitudes of the torques (Fig. 2C) yielded no significant difference within the walking conditions ($P=0.29$) or the running conditions ($P=0.19$).

Shoulder

In both walking and running, θ_{sho} followed a stride-frequency pattern with peak flexion occurring near contralateral heel strike (Fig. 3A,B). The magnitudes of angular excursion tended to be similar within each gait. However, BW tended to shift θ_{sho} towards extension compared with SW, while BR tended to shift θ_{sho} towards flexion compared with SR. τ_{sho} also followed a stride-frequency pattern (Fig. 3C,D), with peak extension torques coinciding with peak shoulder flexion. ANOVA tests showed 33% reduced $\Delta\mathbf{T}_{sho}$ in BW compared with SW ($P=0.0039$), and 32% reduced $\Delta\mathbf{T}_{sho}$ in BR compared with SR ($P<0.0001$) (Fig. 3E).

Elbow

Consistent with the instructions given to the subjects, θ_{elb} was substantially more flexed in BW and BR compared with SW and SR (Fig. 4A,B), and the forearm was close to perpendicular ($\theta_{elb}=1.57$ rad) with the upper arm. Mean θ_{elb} in SW and BW was 0.62 ± 0.02 and 1.54 ± 0.05 rad, respectively ($P<0.0001$). Mean angles were similar in running, with 0.61 ± 0.05 and 1.61 ± 0.10 rad in SR and BR, respectively ($P<0.0001$). Both gaits showed angular excursions occurring at stride frequency. However, unlike in the shoulder, the pattern of θ_{elb} across the stride differed between straight and bent arm conditions. In SW and SR, the elbow flexed near contralateral heel strike, while in BW and BR, the elbow extended at this point. τ_{elb} followed stride frequency patterns for SW and SR, but step frequency patterns for BW and BR (Fig. 4C,D). In addition, mean muscle torques were substantially shifted towards flexion in the bent arm conditions (on average, 1.21 N m in walking and 1.60 N m in running), presumably due to increased gravitational torque. Comparison of magnitudes yielded significant increases in $\Delta\mathbf{T}_{elb}$ for the bent arm conditions compared with the straight arm conditions in both walking (110% increase, $P=0.0037$) and running (30% increase, $P=0.0096$) (Fig. 4E).

Energetics

Fig. 5A shows the results from the energetics data collection on the six-subject subsample. BW incurred an $11\pm3\%$ higher $\dot{V}_{O_2,net}$ than SW ($P=0.0179$), increasing by 0.30 ml O_2 min^{-1} kg^{-1} compared with the normal SW condition. In contrast, $\dot{V}_{O_2,net}$ was the same for the SR and BR conditions ($P=0.63$). Individual oxygen consumption data are presented in Fig. 5B, with the abnormal conditions (BW and SR) expressed as a percentage of the corresponding normal conditions. Five of the six subjects increased their oxygen consumption during abnormal walking; in contrast, four of the six subjects had nearly identical oxygen consumption during abnormal and normal running.

DISCUSSION

The results from our experiment confirm our hypothesis that there is a mechanical tradeoff between τ_{sho} and τ_{elb} when bending the arm
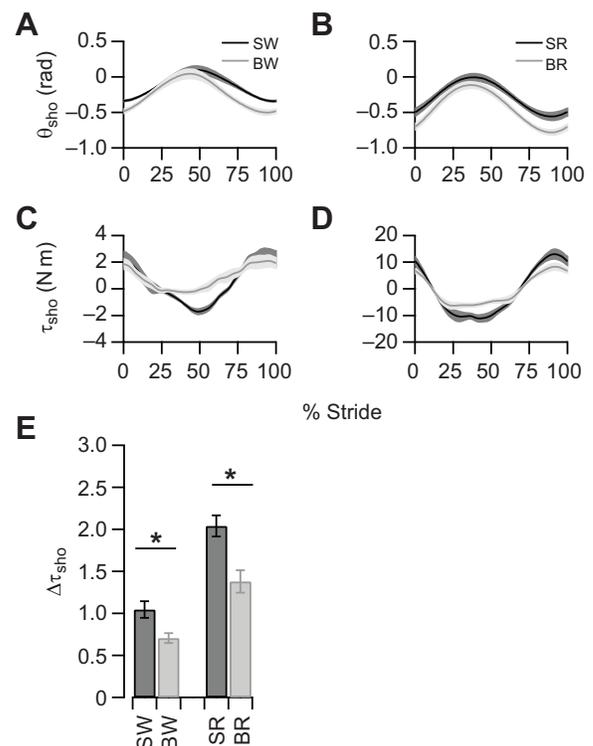

Fig. 3. Comparison of shoulder angles and muscle torques between experimental conditions. (A,B) Shoulder angle (θ_{sho}) across the stride for (A) walking conditions and (B) running conditions. (C,D) Shoulder muscle torque (τ_{sho}) across the stride for (C) walking conditions and (D) running conditions. Shaded bands are ±1 s.e.m. (E) Normalized magnitude of shoulder muscle torque ($\mathbf{T}_{sho}$). Error bars are ±1 s.e.m. Asterisks indicate statistically significant differences ($P<0.05$) between straight arm and bent arm conditions within each gait. SR/SW, straight arm running/walking; BR/BW, bent arm running/walking.
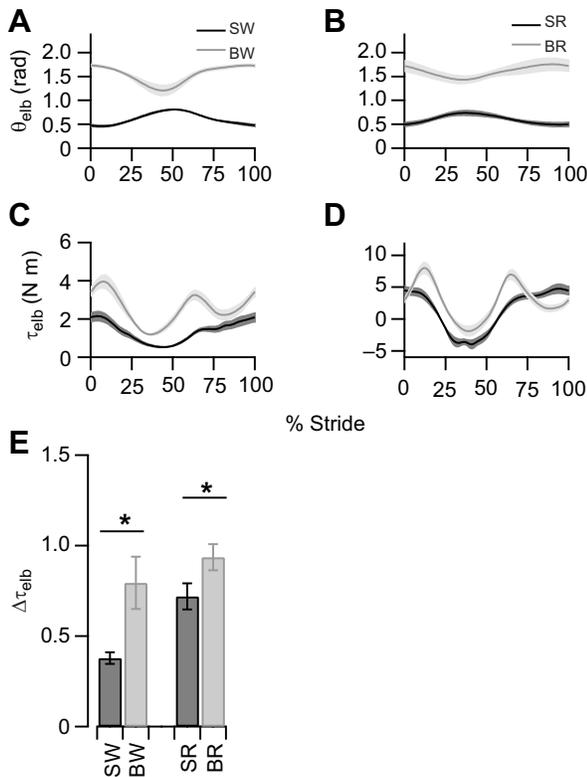
Fig. 4. Comparison of elbow angles and muscle torques between experimental conditions. (A,B) Elbow angle (θ_{elb}) across the stride for (A) walking conditions and (B) running conditions. (C,D) Elbow muscle torque (τ_{elb}) across the stride for (C) walking conditions and (D) running conditions. Shaded bands are ±1 s.e.m. (E) Normalized magnitude of elbow muscle torque (T_{elb}). Error bars are ±1 s.e.m. Asterisks indicate statistically significant differences ($P<0.05$) between straight arm and bent arm conditions within each gait. SR/SW, straight arm running/walking; BR/BW, bent arm running/walking.

Fig. 5. Net oxygen consumption during walking and running with different elbow angles. (A) Comparison of mass-specific oxygen consumption ($\dot{V}_{O_2,net}$) between straight arms and bent arms in walking and running. Error bars are ±1 s.e.m. Asterisk indicates a statistically significant difference ($P=0.0179$) between straight and bent arm conditions within a gait. (B) Oxygen consumption of abnormal arm configuration conditions, expressed as a percentage of the normal arm condition. Open symbols represent six individual subjects that participated in the data collection. Dark lines are the inter-subject means, with shaded bands representing the 95% confidence interval of the mean. SR/SW, straight arm running/walking; BR/BW, bent arm running/walking.

at the elbow during locomotion. Bending the arm reduced the relative magnitude of the shoulder muscle moment in both walking and running (Fig. 3E), while simultaneously increasing the relative magnitude of the elbow muscle moment (Fig. 4E). Our hypothesis focuses on the vertical external forces that cause an external torque on the forearm resisted by τ_{elb}. The stride time series of τ_{elb} (Fig. 4C,D) shows the effect of bending the elbow and bringing the forearm more perpendicular to the net vertical external force. In BW and BR, τ_{elb} showed a step frequency pattern similar to vertical accelerations of the trunk (Kubo et al., 2004; Thorstensson et al., 1984). Conversely, τ_{elb} oscillated at stride frequency in SW and SR, likely due to swinging of the upper arm (Fig. 3A,B) dominating the external torque acting on the forearm.

We predicted that the gait-specific stereotypical behaviors of straight arm walking and bent arm running are driven by the energetic consequences of the mechanical tradeoff, with walking favoring straight arms and running favoring bent arms. The first part of our prediction was supported by our data (Fig. 5), as walking with a bent arm increased $\dot{V}_{O_2,net}$ by 11%, similar to the magnitude of cost increase caused by restricting arm swing (Bruijn et al., 2008; Collins et al., 2009; Umberger, 2008; Arellano and Kram, 2014). However, our results indicate equivalent $\dot{V}_{O_2,net}$ between the two running conditions (Fig. 5), which does not support our energetic hypothesis for running. The existence of an energetic tradeoff favoring bent arms in running cannot be ruled out for several reasons. It is possible the effect size of bending the arm on energetics is too small to be
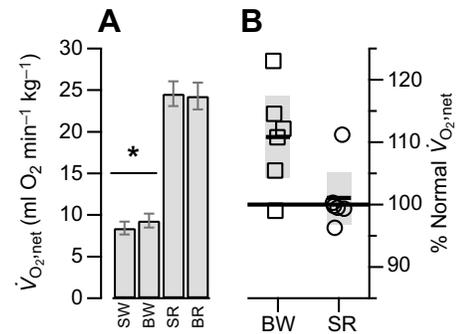
statistically distinguished in our relatively small sample of six individuals. A second possibility is that differences in energetic cost were masked by a shift in metabolic substrate utilization yielding the same oxygen consumption (Fletcher et al., 2009), although the greatest shifts occur at the upper limits of aerobic capacity rather than the comfortable running speed tested here (Goedecke et al., 2000). Finally, we only tested a single dimensionless speed, and it is possible that running becomes less costly with bent arms than straight arms at higher speeds than tested here. Although elbow angle did not affect the net oxygen cost of running, higher torques were generated by the shoulder muscles with straight arms than with bent arms, requiring more activated muscle volume. Larger and costlier motor units tend to be activated as more volume is recruited in muscle contractions (Duchateau and Enoka, 2011), so it is possible that fiber recruitment order affects the tradeoff at faster speeds.

Optimal energetics appears to be the reason why straight arms are stereotyped during walking, but the reason for stereotyped bent arm running remains unclear. Although we have focused on energetic cost as a mechanism in this study, stereotypical bent arm running may result from a non-energetic benefit. For instance, the biceps muscle is thought to link the inertia of the forearm and the head during running for the purpose of head stabilization (Lieberman, 2011); bent arms increases the flexion moment at the elbow and therefore may provide a head stabilization benefit. We must also consider that the stereotyped behavior during running may not provide a benefit at all; there was much greater variation within our sample in average θ_{elb} for the normal running condition (s.d. of 0.274 rad) than for the normal walking condition (s.d. 0.070 rad), matching our anecdotal observation that runners use quite varied forearm positions.

One potential benefit we did not test in this study is that bent arm running optimizes the relative energetic costs of the shoulder and elbow muscles, independent of the total cost of arm swing. Straight arm running results in greater τ_{sho}, requiring a greater volume of activated shoulder muscle. More activated volume leads to faster rates of glycogen depletion and lactic acid buildup, both of which are key physiological factors in muscle fatigue (Baker et al., 1993; Maclaren et al., 1989). Therefore, bent arm running may increase time until fatigue in the shoulder muscles even if the total energetic cost of the

two arm configurations is the same. The evolution of endurance running in the genus *Homo* was a major transition in the course of human evolution (Bramble and Lieberman, 2004). The capacity to run very long distances at speeds that force galloping in prey mammals was a critical innovation in hunter–gatherer ecology. Staving off shoulder muscle fatigue may benefit long-distance running and provided the mechanism for the typical human behavior.

Finally, our results have implications for the evolution of arm proportions in hominins. Arm length relative to leg length was greater in *Australopithecus* and in *Homo habilis* than in modern humans (Young et al., 2010), as was forearm length relative to upper arm length (Churchill et al., 2013; Richmond et al., 2002). Modern arm proportions emerged in *Homo erectus*, and coincided with the evolution of endurance running as an important hominin behavior (Bramble and Lieberman, 2004). Reductions in forearm length and total arm length should reduce τ_{elb} and τ_{sho}, respectively, and therefore may be signals of selection for lesser arm swing costs during endurance running. Selection for running may have been an important factor shaping the evolution of hominin arms.

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