Balancing stability and mobility during overhead motion: Lessons from the bat shoulder

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INTRODUCTION: Repetitive overhead motion in humans often leads to shoulder injuries, a consequence of an evolutionary trade-off in which the glenohumeral joint's bony anatomy provides minimal stability constraints, but placing greater stress on the joint's surrounding soft tissues. Traditional animal models used to study shoulder pathology are quadrupeds, and lack comparable capacity for overhead motion. In contrast, bats consistently engage in overhead motion during flight, subjecting their shoulders to substantial loading throughout their relatively long lifespan. Remarkably, the biomechanical demands placed on a bat's shoulder are estimated to exceed the cumulative shoulder loading endured by a competitive swimmer by 45-fold [1,2]. In this study we were inspired to study functional adaptations in the shoulders of bats, the only mammals that use overhead motion as a critical part of their function and share similar coracoacromial arch anatomy with humans. We performed comparative anatomy studies of the bat shoulder compared to the mouse shoulder, a similarly-sized quadruped. We quantified the constraints imposed by the bony anatomy of bats to maintain joint stability and determined the adaptations of rotator cuff tendons that allow bats to sustain overhead motion in a high stress repeated loading environment.

METHODS: _Sample preparation:_ All animal procedures were approved by the Columbia and Brown University Institutional Animal Care and Use Committees. Shoulders harvested from adult (12 weeks) C57BL6/J mice (n=6) and C. perspicillata bats (n=6) were dissected and fixed in three different positions: full shoulder extension ("P1"), intermediate ("P2"), and full shoulder flexion ("P3"). To consistently identify the angle between the scapular spine and the humerus for each fixation position, gait (mouse) and flight (bat) analyses were used. _MicroCT Imaging:_ Samples were scanned at 55 kV peaks with 145 mA intensity, and 19.3 μm resolution (Skyscan 1272, Bruker). _Anatomical Measurements:_ Images were reconstructed (NRecon, Skyscan), and bone parameters were measured (Skyscan CT Analyzer). The scapular linear index was determined as the ratio of scapular width to length. Supraspinatus and infraspinatus linear indices were calculated using the length from the medial aspect of the spine to the superior or inferior angle. Glenoid retroversion was measured via the anterior facing angle between the body of the scapula and the glenoid face on the axial cross section. Supraspinatus outlet area was measured as the area posterior to the coracoid, inferior to the acromion, and within the acromial arch. Glenoid curvature was measured using the circle tool in ImageJ. The arc length of the glenoid was calculated using the angle from the superior to the inferior glenoid rim. _Biomechanics:_ Humerus and supraspinatus muscle and tendon units were dissected from adult (8 weeks) C57BL6/J mice (n=4) and C. perspicillata bats (n=5). To determine cross-sectional area of the tendon, microCT scanning was performed at 55 kV peaks with 145 mA intensity, and 6.5 μm resolution (Skyscan 1272, Bruker). Following scanning, samples were preconditioned by being sinusoidally loaded from 0.05 to 0.2 N for 5 cycles then allowed to rest for 2 minutes, before being strained until failure in tension at 0.1 %/s. _Mathematical model:_ We developed a model of shoulder instability as a function of the glenoid and humerus curvature and insertion angle of rotator cuff tendons. To model response to destabilizing forces, a concentrated force F was applied quasistatically, until the humeral head became unstable. To calculate the resistance of the system to instability, the work U done by F up to the point of instability was calculated: $U = \int \vec{F} \cdot d\vec{r}$, where $d\vec{r}$ is the increment of path length followed by the point of application of the force. Equations were solved using Matlab (The MathWorks). _Statistical Analysis:_ Statistical analysis was performed using unpaired t-tests with Welch's correction (GraphPad Prism 7). The threshold for statistical significance was defined at $p < 0.05$.

RESULTS: _Bony Anatomy:_ The scapular index and infraspinatus index were both significantly larger in bats than in mice, while the supraspinatus index did not differ (Fig. 1a). The supraspinatus outlet area was significantly greater in bats compared to mice (Fig. 1b). The glenoid was retroverted in bats and anteverted in mice (Fig. 1c). Glenoid curvature and arc length were significantly higher in bats than in mice (Fig. 1d). _Tissue level mechanics:_ The supraspinatus tendon in bats had a significantly higher cross-sectional area (CSA) compared to those of mice. In contrast, for the infraspinatus tendons of the two species, there was no significant difference in CSA (Fig. 2a). Bat supraspinatus tendons showed significantly lower failure stress compared to mice, but bats infraspinatus tendons showed a significantly higher failure stress than mice (Fig. 2b). Bat supraspinatus tendons had a significantly lower modulus compared to mice, but there was no difference in the modulus of the infraspinatus tendons when comparing bats to mice (Fig. 2c) Bat supraspinatus tendons were significantly less resilient than those of mice, while their infraspinatus tendons were significantly more resilient (Fig. 2d). _Modeling:_ The bat shoulder was stable over a dramatically larger range of angles compared to the mouse shoulder (Fig. 3).

DISCUSSION: The bat's enlarged infraspinatus index suggests a larger role for the infraspinatus in the bat's glenohumeral stability. This also implies adaptations to relieve stress on the supraspinatus. Similarly, the larger supraspinatus outlet in the bat provides more space for the supraspinatus to pass under the coracoacromial arch to prevent supraspinatus shoulder impingement, commonly seen in overhead-throwing athletes [3]. The glenoid was anteverted in mice, whereas it was retroverted in bats, analogous to the retroverted glenoids reported in high-level overhead-throwing athletes [4]. The bat glenoid had a larger glenoid arc length and articulating surface area with the humeral head, thus providing more bony stability to the joint. Bat supraspinatus tendon cross-sectional area was significantly larger than that of mice, consistent with previous measurements of supraspinatus-acromion clearance and outlet area. While bat supraspinatus tendons were weaker when compared to mice, as indicated by significantly lower maximum failure stresses, stiffness and toughness, bat infraspinatus tendons were significantly tougher and more resilient. The energy needed to dislocate the humeral head of bats was substantially larger than that in mice and stability was seen for a larger range of shoulder angles. Taken together, these results suggest that evolutionary adaptations in bats led to reduced stress on the supraspinatus, thus reducing risk of catastrophic tendon rupture, while the infraspinatus compensated by playing a stabilizing role.

SIGNIFICANCE: Functional adaptations of the bat's shoulder joint provide insight into developing new approaches to treat glenohumeral joint instability.

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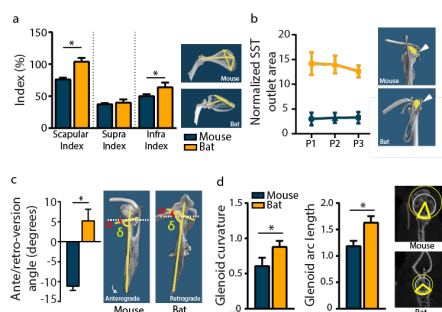
Figure 1. (a) Scapular, supra. and infra. indices (b) Supraspinatus outlet area (c) Glenoid version (d) Glenoid curvature and arc length
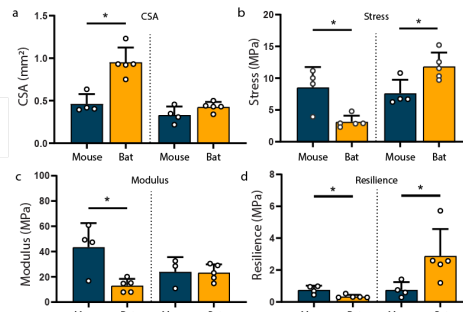

Figure 2. Material properties of bat and mouse supraspinatus (left) and infraspinatus (right) tendons
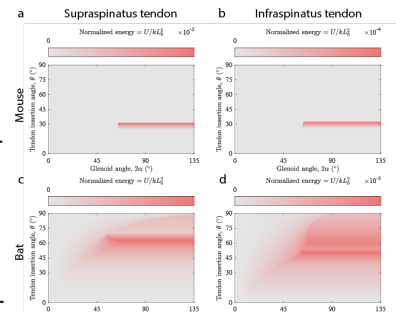

Figure 3. The energy barrier that resists shoulder instability (red) was substantial in bats (bottom) over a larger range than in mice (top).