ISB 2013 BRAZIL
XXIV CONGRESS OF THE INTERNATIONAL SOCIETY OF BIOMECHANICS
XV BRAZILIAN CONGRESS OF BIOMECHANICS

STATICS OF THE BAT SHOULDER GIRDLE IN THE MID-DOWNSTROKE

[1]Alexander N. Kuznetsov and [1,2]Aleksandra A. Panyutina
[1]Department of Vertebrate Zoology, Faculty of Biology, Lomonosov Moscow State University, Moscow, Russian Federation
[2]email: myotis@mail.ru

SUMMARY

The complete biomechanical analysis of the mechanical work of the shoulder girdle muscles in a flying bat needs as its integral part a force vector analysis, which was never performed before. We present a simple preliminary graphic analysis of presumable force vectors for the mid-downstroke, when the aerodynamic forces on the wing reach their maxima, and the forces of gravity and inertia of the wing can be neglected.

The bat wing membrane is composed of two evolutionary and biomechanically distinct parts. The proximal part, which we call "archeopatagium", is stretched between the fore and hind limbs and transfers part of the aerodynamic force applied to it onto the humerus along the membrane skin. The distal part, neopatagium, due to greater surface area and aerial speed, is subject to much greater aerodynamic forces, which are transferred via fingers. The forces from archeopatagium and neopatagium act on the forelimb almost at right angles to each other, and so their balance at the shoulder girdle can be treated separately.

Our analysis have shown that the clavicle acts as a strut and that pectoralis, serratus ventralis thoracis and acromiotrapezius muscles are most important for the shoulder girdle balance in the bat mid-downstroke. We have uncovered the biomechanical reason for hypertrophy of serratus ventralis thoracis muscle and unique shift of its insertion from the dorsal scapular edge onto the caudal one together with the caudal elongation of scapula.

INTRODUCTION

The complete biomechanical analysis of the mechanical work of the shoulder girdle muscles in a flying bat needs electromyographic data, X-ray filming for kinematics and force vector analysis. By now there are few articles on the electric activity of the shoulder girdle muscles [1-5], very few articles on the shoulder girdle kinematics [5-8], and no articles on statics. Here we try to partially fill this gap.

METHODS

The simple graphic analysis of presumable force vectors was performed for the mid-downstroke (i.e. horizontal) position of the generalized bat wing. In this phase of the wing beat cycle the aerodynamic forces applied to the wing reach their maxima, and the forces of gravity and inertia of the wing can be neglected. So, the task of analysis is to find the muscular forces, which would equilibrate the aerodynamic ones.

In contrast to birds, the bat wing is composed of two biomechanically and evolutionary distinct parts, and the aerodynamic forces applied to these two cannot be simply summed up (Figure 1). One part is the proximal membrane stretched between the fore and hind limbs. We call it "archeopatagium", because it was already developed in the bat ancestors as it is in the flying squirrels, flying lemurs and gliding marsupials. The aerodynamic force Fa acting upon archeopatagium is divided between the fore and hind limbs, and pulls the humerus posteriorly via the skin of the membrane by force component Fa_{fl} (the opposite component Fa_{hl} pulls the hindlimb anteriorly). Beyond the elbow, the membrane is associated with the fore limb only, being supported by its fingers. We call it "neopatagium". It has greater surface area and aerial speed than archeopatagium, and hence, is subjected to much greater aerodynamic force Fn. It is transferred onto the forelimb mainly via the 5th finger, not via the skin, in contrast to Fa_{fl}. Since Fa_{fl} lies approximately in the neopatagium plane and Fn is perpendicular to it, we can treat the two forces separately.

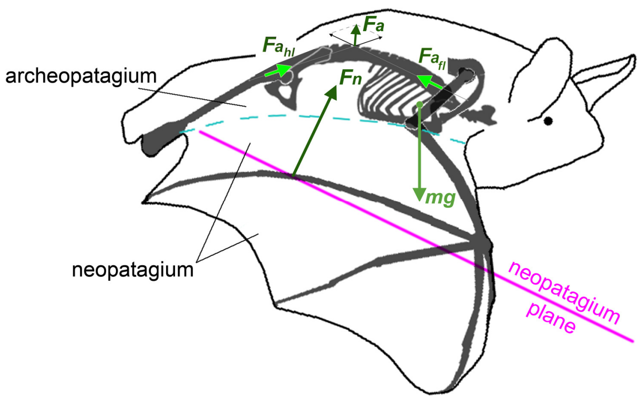

Figure 1: Aerodynamic forces applied to archeopatagium and neopatagium in the mid-downstroke.

The force magnitudes were estimated as follows. In flapping flight, the upstroke does not produce lift and is about 1.5 times shorter in bats than the downstroke. So, the mean sum of Fa and Fn on each wing is required to be ~$0.83mg$ to counterbalance gravity momentum of the whole cycle. In the mid-downstroke the sum may reach 1*mg*. The *Fa* to *Fn* ratio was deduced from the surface areas of the parts of membrane and their relative aerial velocities which increase linearly in distal direction. Fa_{fl} was deduced from *Fa* taking into account the typical curvature of the membrane profile.

RESULTS AND DISCUSSION

Consider the effect of *Fn*, which points at right angles to the neopatagium plane (Figure 2). Here, for all of the shoulder girdle elements, we take into account only force components, which are perpendicular to this plane (all force components situated in this plane will be analyzed on Figure 3). Under conditions of equilibrium in joints of the free limb, all of its segments, together with the scapula, can be considered following the rules of theoretical mechanics as an indivisible monolith (so-called principle of solidification). Its distal part leans on air with the force *Fn* and the proximal part leans on the clavicle. Bats have only two muscles which can balance the wing relative to a straight line (*a*) connecting the point of application of the force *Fcl* of response of the clavicle to the acromion with the point of application of *Fn*. These are the pectoralis (force *Fp*) and serratus ventralis thoracis (force *Fs*) muscles; other muscles of the shoulder girdle have negligible vertical force components. The lines of action of *Fp* and *Fs* pass anterior and posterior to the line (*a*), respectively. The wing equilibrium requires colinearity of the resultant of *Fp* and *Fs* on the one hand, and the resultant of *Fn* and *Fcl* on the other (line (*b*) is the intersection of the plane containing *Fn* and *Fcl* and the plane containing *Fp* and *Fs*).

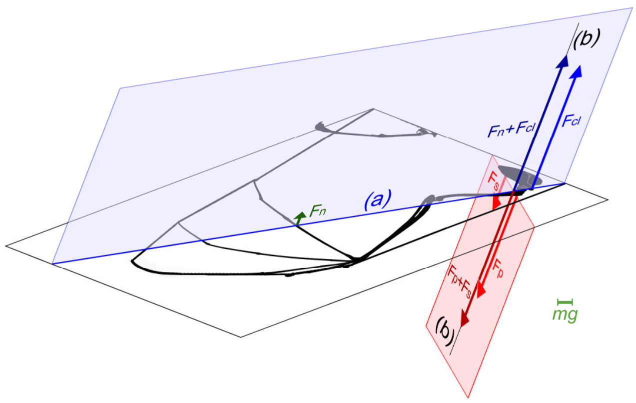

Figure 2: Forces perpendicular to the neopatagium plane.

Consider now the balance in the neopatagium plane (Figure 3). *Fn* has no projection on it by definition. The vector sum F_1 of Fa_{fl} and *Fp*, with the help of intrinsic shoulder joint muscles (which consideration is beyond the scope of this note), is transferred via humeral head onto scapula, tending to shift it caudomedially. The displacement, which could be caused by this force, is prevented by the craniolaterally inclined clavicle, which exerts the force *Fcl* on the acromion; *Fcl* with F_1 gives the vector sum F_2 pointing laterally. The last is in turn counterbalanced by a pair of forces *Fatr* and *Fs* of acromiotrapezius and serratus ventralis thoracis muscles, respectively.

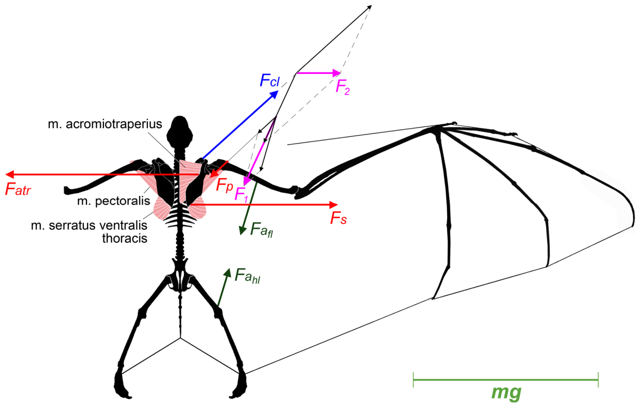

Figure 3: Forces in the neopatagium plane.

Noteworthily, the vertical component of *Fs* is more than twice greater than its horizontal component (see scale bars on Figures 2 and 3). To gain this vertical component of the force, which is particularly significant for flapping flight, the insertion of serratus ventralis thoracis muscle has shifted in bats from the dorsal (medial in bat and human terminology) to caudal (lateral) edge of the scapula.

Ideally, the vector sum of the two *Fcl* components, i.e. the component in the neopatagium plane (Figure 3) and the component perpendicular to it (Figure 2), should coincide with the longitudinal axis of the clavicle, and thus pass through the sternoclavicular articulation. In this case, the clavicle undergoes strictly longitudinal compression. If the vector sum of these components does not coincide with the longitudinal axis of the clavicle, the balance of forces in the sternoclavicular articulation can be provided by the clavotrapezius and subclavius muscles.

CONCLUSIONS

Though simple, our analysis gives *raison d'être* for the major peculiarities of the bat shoulder girdle myology, such as hypertrophy of serratus ventralis thoracis muscle and unique shift of its insertion from the dorsal scapular edge onto the caudal one together with the caudal elongation of scapula. This is necessary to balance the aerodynamic force applied to neopatagium.

The involvement of the shoulder girdle muscles in the mid-downstroke, which follows from our analysis, appears to be in a good accordance with the most reliable electromyographic data [3,4]. However, for muscular mechanical work consideration, a quantitative 3D force analysis is necessary, and not only in the mid-downstroke but throughout this phase. We are going to perform such analysis with the help of CT scans of frozen bats in the nearest future.

REFERENCES

1. Kovtun MF, Moroz VF. Study of the bioelectric activity of the shoulder girdle muscles in *Eptisicus serotinus* Schreb. (Chiroptera). *Dokl AN SSSR*. **210**:1481-1484, 1973 (in Russian).
2. Kovtun MF, Moroz VF. Electromyographic study of activity of flight muscles in *Myotis myotis* (Chiroptera). *Dopov AN URSR Ser B*. **7**:651-653, 1974 (in Ukrainian).

3. Hermanson JW, Altenbach JS. The functional anatomy of the shoulder of the pallid bat, *Antrozous pallidus*. *J Mammal*. **64**:62-75, 1983.
4. Hermanson JW, Altenbach JS. Functional anatomy of the shoulder and arm of the fruit-eating bat *Artibeus jamaicensis*. *J Zool*. **205**:157-177, 1985.
5. Altenbach JS, Hermanson JW.. Bat flight muscle function and the scapula-humeral lock. In: Fenton MB, Racey P, Rayner JMV. *Recent Advances in the Study of Bats*, Cambridge University Press, Cambridge. 100-118, 1987.
6. Hermanson JW. Functional morphology of the clavicle in the pallid bat, *Antrozous pallidus*. *J Mammal*. **62**:802-805, 1981.
7. Panyutina AA, Korzun LP, Kuznetsov AN. Kinematics of the Shoulder Girdle in Bats. *Dokl Biol Sci*. **439**:240-243, 2011.
8. Panyutina AA, Kuznetsov AN, Korzun LP. Kinematics of chiropteran shoulder girdle in flight. *Anatomical Rec*. 2013 (in press).