Flight Control Mechanisms in Pterosaurs

CHATTERJEE, Sankar\textsuperscript{1}, LIND, Rick\textsuperscript{2} and YOUNG, Rocky\textsuperscript{1}

Flight, for biological systems and man-made systems, requires both lifting mechanisms and control mechanisms. Actually, the generation of lift is traditionally much easier than the control of the resulting flight. Mesozoic pterosaurs evolved several control mechanisms that were instrumental to their survival as a species. These pterosaurs ranged in size from a sparrow to a small aircraft and were highly aerial acrobats during the Mesozoic. Flight imposes limitations on size and body weight. Smaller pterosaurs could hover, medium-sized could flap for continuous level flight, while the largest groups were primarily soarers (Chatterjee and Templin, 2004).

The components of the integrative biological systems of controls are beginning to emerge from recent study of animal locomotion (Dickinson et al. 2000). Both neural and mechanical feedback play roles in controlling animal flight. Rapid feedback from both mechanical and neural pathways is integrated with information from eyes, ears, noses, and other sensing organs used to control overall flight motion of an animal and provide robust operation in a wide variety of environments. Here we investigate control of flight in pterosaurs using neurosensory, biomechanical, and computer simulation data.

Flight requires fine coordination between muscles and senses to maintain stability. The pterosaur brains, as reconstructed from digital endocasts, are relatively small, but show some birdlike attributes and internal connectivity in response to aerial adaptation (Witmer et al., 2003). The visual resolving power of pterosaurs was greatly improved as is evident by the enlargement of their optic lobes, which resulted in broad, overlapping binocular vision for distance judgment during foraging.

The inner ear of pterosaurs, in addition to sensing sound, contains gravity and rotation sensors in the forms of semicircular canals. The vestibular apparatus containing three semicircular canals, which are oriented roughly in the three planes of space, function as a well-developed system for sensing rotational acceleration and equilibrium like a gyroscope during flight. The enormous flocculus at the center of the canalicular system has important neural integration with the vestibular system, the eye muscles, and the neck muscles for stabilizing gaze without blurring vision during maneuvers (Witmer et al., 2003). The neural canal shows increased diameter in the cervical and lumbar region, which might be linked to locomotor control of both wings and the hindlimbs. Flow of neural information to and from the wing and the brain apparently increased for the flight as well as hindlimb innervations for terrestrial locomotion. As in other vertebrates, the spinal cord in pterosaurs probably gave off paired spinal nerves, each with two roots, a dorsal sensory and a ventral motor roots. There are two distinct enlargements in the spinal cord in the cervical and lumbar regions, each associated with nearby brachial plexus and lumbosacral plexus for controlling sensorimotor system of the wings and legs respectively.

Pterosaurs had a unique wing anatomy unlike that of birds and bats where the forelimb and the hyper-elongated fourth finger formed a single bony spar at the leading edge to support long and narrow membranous wing that extended along the sides of the body to the legs. Like modern tailless aircrafts, pterosaurs had all their control surfaces on their main wing membrane, which was controlled by fore- and hindlimbs, as well as by tail in basal forms. Most pterosaurs had high-aspect ratio wings like those of modern seadbirds. These wings are long, narrow, flat, and pointed with low wing loading and low cruising speed that are efficient for soaring in open airspace by exploiting updraft (Chatterjee and Templin, 2004). The wings were extremely flexible at various joints so that they could morph their shape and position instantly to best suite changing flight conditions. They could flap one

\textsuperscript{1}Museum of Texas Tech University, Lubbock, Texas 79409, USA

\textsuperscript{2}Mechanical and Aerospace Engineering, University of Florida, Gainesville, Florida 32611, USA

E-mail: sankar.chatterjee@ttu.edu
wing more forcefully than the other or change the angle of flapping between the two wings. Called thrust vectoring to monitored changes in flying conditions. Pterosaur wing bones possess many more independently controllable joints (such as metacarpal and pteroid segments) than those of birds and bats, which were integrated to produce complex and functionally dynamic wing conformations. Moreover, the wing finger could be folded and extended automatically without much muscular effort as it was coupled with the elbow joint (Prondvai and Hone, 2008). This ingenious design enabled the pterosaurs to fold and conceal its wings against its body when not in use, or changes the wingspan to reduce drag and increase speed during flight when swept back.

The pterosaur wings had relatively flat camber with streamlined spar but had developed several control devices analogous to flap, slat, aileron, elevator, fin, rudder, and horizontal stabilizer of an aircraft (Chatterjee and Templin, 2012). The orientation of pterosaur’s flexible pteroid bone is controversial. Either it was directed forward (Wilkinson et al., 2005), or it was oriented medially in a more stable position (Palmer and Dyke, 2009). No doubt, the pteroid bone served to move the propatagium up and down to change the camber and the wing’s angle of attack and support the outboard end of a leading edge flap. The cambered propatagium would facilitate not only during takeoff by producing high lift, but also during landing as it acted as an airbrake to increase drag and reduce the stalling speed. Pterosaur wing had ‘leading edge’ technology like that of large modern aircraft to fly at much lower speeds without stalling. Similarly, multi-slotted inner fingers correspond to slats on the wing of an aircraft, which suppress flow separation at the location where wing sweepback may be controlled. Ailerons, the movable surfaces of the aircraft wing trailing edges near the tips, are deflected in opposite direction for roll and control in turns. In pterosaurs, differential twisting or washout in both wingtips would function like ailerons during banking. The complete uropatagium between the hindlimbs and the long tail in ‘rhamphorhynchoids’ could function as an elevator of an aircraft by increasing tail-induced camber and pitching moment.

Sensing the flow of air over the body can be useful information to a flyer for finer adjustments of wings to maintain its intended flight direction. The wing membrane of pterosaurs was covered with hairlike structures both on dorsal and ventral surfaces that might have acted as mechanoreceptors like those of insects, birds, and bats (Dudley, 2000; Brown and Fedde, 1993; Sterbing-D’Angelo et al., 2011). Perhaps, pterosaurs could sense the speed and direction of the airflow over the wing with the help of hairlike structures. The tactile senses on hindlimbs and tail would also be valuable for downwash—flow of air forced downward by the wings. Such information is equivalent to sensing the amount of lift produced by the wing. These tactile receptors associated with these hairs were possibly involved in sensorimotor flight control by providing aerodynamic feedback like those of insects, birds, and bats. The feedback responses will direct muscles to alter the wing shape to an optimal position. The enlarged flocculus might have acted as an autopilot device to process proprioceptive and other sensory information from the wing that stretched between the limbs, as well as with limb joint themselves, thus having a more direct impact on flight control (Witmer et al., 2003). Vision, equilibrium sensing, and airflow sensing were apparently used at all levels in pterosaurs as a flight control system.

Pterosaurs evolved two basic wing planforms over time similar to the condition of bats: (1) the basal ‘rhamphorhynchoids’ had broad wings with a complete uropatagium between the hindlimbs and the long tail; and (2) in pterodactyloids, with the loss of the bony tail, the uropatagium is split in the middle, becomes narrow, so that each leg could move independently to change the geometry of the cheiropatagium, thus improving the flight performance and terrestrial locomotion (Unwin, 2006). There appears to be a shift from tail-induced wing control to leg-induced wing control during the evolution of pterosaurs. With the loss of the tail, the pterodactyloids became more acrobatic and maneuverable than ‘rhamphorhynchoids’ but became less stable; instability was probably compensated
by the neural control (Maynard Smith, 1952), leg-induced control, and the development of large cranial crest. The crest functioned as a front rudder to make agile turn (Chatterjee and Templin, 2012; Roberts et al., 2011). This advantage of large cranial crest comes with a tradeoff, which is a decrease in the pterodactyloid’s stability.

References


