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Bird Flight: Insights and Complications

New techniques show that more than the wing participates in flying

G. E. Goslow Jr., K. P. Dial, and F. A. Jenkins Jr.

"To attain to the true science of the movement of birds in the air, it is necessary to give first the science of the winds. . . .¹ You will study the anatomy of the wing of a bird, together with the muscles of the breast which are the movers of these wings."²

Leonardo da Vinci
ca. 1500 A.D.
(Hart 1961)

Leonardo da Vinci, in his quest to achieve artificial flight, kept notes for 25 years on his observations of birds. He was convinced that a thorough understanding of how birds fly would lead him to the fundamental principles necessary to fulfill his dream that man could achieve "flapping flight" using his own muscular system. Unfortunately, this vital misconception was not realized until late in life (Gibbs-Smith 1978). Leonardo's studies of flight centered on hours of observation, detailed dissections, and examination of the wings of a variety of species. His approach was sound, and his accomplishments, diversions, and failures foreshadowed the course of scientific investigation today.

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Only through studies of flight in modern species can we reconstruct its evolution

The movements of birds during flight have inspired the human imagination for centuries. Scientific descriptions of the skeleton of the wing and the muscles that move it were begun early in this century (Fürbringer 1902) and continue to be made today (for a review see Raikow 1985). Much has been learned about the physical parameters that influence a wing's performance (Pennycuik 1968, Rayner 1988), the relationship of wing shape to habitat and mode of flight (Greenewalt 1962, Savile 1957), and the subtleties of wing movement during upstroke and downstroke as revealed by slow-motion photography (Brown 1963, Nachtigall 1980, Rüppell 1977). Nevertheless, due to the complexity of its design and of the movement patterns during a wingbeat cycle, knowledge of the bird wing remains sketchy and incomplete.

Little is known, for example, about the nerve cells that control the muscles, the behavior of the muscles themselves, and the role of the skeleton during flapping flight. An ex-

panded technology has recently provided the first glimpses into these issues.

We initiated a series of empirical studies four years ago of two common species of birds, the domestic pigeon (*Columba livia*) and the European starling (*Sturnus vulgaris*), which have contrasting flight styles. Our initial objectives seemed straightforward. We planned to provide a database for clarification of the neural control of the wing, biomechanics of the wing and shoulder, and evolution of flapping flight. As was the case for Leonardo da Vinci, we not only gained new insights into bird flight, but we were confronted with unexpected results that required further investigation. In this article, we review some of our studies of the design of the pectoralis, the primary depressor muscle of the wing, as it relates to wing control. We also describe the movements of the shoulder girdle (those bones that support the wing against the body) and thoracic elements during flight.

The pectoralis

Flapping flight entails a downstroke, when the wing is brought downward and forward to provide thrust, and an upstroke that prepares the wing for the subsequent downstroke. The wingbeat cycle (Figure 1) can be divided into four phases: upstroke-downstroke transition, downstroke, downstroke-upstroke transition, and upstroke.

The pectoralis might appear at first glance to be a simple depressor of the

¹Ms. E., fol. 54 r.

²Codex Atlanticus, 45 r.

wing. Inspection of this muscle reveals, however, several features that are indicative of a complex organization.

First, in many birds (including pigeons and European starlings) the large pectoralis is divided into two portions by a sheet of connective tissue that runs through the muscle (labeled MI in Figure 2; Simić and Andrejević 1963, Vanden Berge 1979). The portion of the pectoralis that is located in front of (rostral to) and to the side of (lateral to) the sheet is the sternobrachialis (SB), and the portion behind (caudal to) and to the inside of (medial to) the connective tissue sheet is the thoracobrachialis (TB). The names relate to the origin (fixed end) of these muscles from the sternum and thorax, respectively, and to their insertion (movable end) onto the brachium or upper arm. The SB and the TB appear to be distinctive from one another in that the muscle fiber bundles that comprise the SB are aligned in a direction different than that of the bundles of the TB.

Second, the tendons (structures that connect the muscle fiber bundles to the bone) of the SB and TB attach to different skeletal structures. Finally, the SB and TB appear to be innervated by separate nerve branches arising from the large group of nerves that course from the spinal cord into the limb (Figure 2b).

Functional subunits: evidence from anatomy and physiology. Initially, we wanted to establish that the primary nerve branches associated with the SB and TB actually innervated each respective part. A glycogen depletion technique was used. When the nerve to a muscle is stimulated continuously, the muscle cells that it innervates eventually undergo anaerobic contractions by using glycogen as their energy supply, and they eventually deplete this fuel store. If those muscle cells are subsequently stained for the presence of glycogen, there is no uptake of stain. Muscle fibers that have not been stimulated, in contrast, remain rich in glycogen and stain a bright pink.

In several anesthetized pigeons, the rostral and caudal nerves to the SB and TB parts of the pectoralis were isolated and, indeed, stimulation of the cranial nerve branch resulted in

Figure 1. Phases in the wingbeat cycle of the European starling (*Sturnus vulgaris*) based on cineradiographic analysis in dorsal (top) and lateral (bottom) views. a. Upstroke-downstroke transition. b. Mid-downstroke. c. End of downstroke. d. Mid-upstroke. In the dorsal series, note the spreading of the furcula (and coracoids). The lateral series depicts the excursion of the sternum relative to the bird's spinal column and a horizontal plane. (After Jenkins et al. 1988.)

Figure 2. Anatomy of the pectoralis muscle in the domestic pigeon (*Columba livia*). a. Lateral view of the pectoralis (the major depressor of the wing) to illustrate its division into the sternobrachialis (SB) and the thoracobrachialis (TB) by a connective tissue sheet, the membrana intramuscularis (MI). b. Deep view of the pectoralis (reflected) and nerves. Fiber bundles of the SB originate on the furcula and ventral surface of the keel of the sternum. The TB arises from the body of the sternum, two thin membranes, and their surrounding bony processes. Some of the fiber bundles of the SB and TB insert on the MI (from contrasting angles) as well as on the humerus. Distinct rostral and caudal nerve branches that arise from spinal nerves X–XII innervate the SB and TB.

Figure 3. Large and small muscle fibers in the pectoralis of *Columba livia*. Photomicrograph is a frozen section (20 μm) from the SB, stained for myofibrillar ATPase after acid preincubation (pH 4.35). The small fibers are numerous and tend to be surrounded within the connective tissue boundary (FB) by the relatively large fibers. (After Dial et al. 1987.)

glycogen depletion of the muscle fibers of the SB. In contrast, the caudal nerve bundle was shown to primarily innervate the TB (Kaplan and Goslow 1989).

The actions of the SB and TB were studied in anesthetized pigeons by placing the wing in a flight position (as determined from films), stimulating each of the two nerves in turn, and employing a force transducer interfaced to an oscilloscope to sense the moment of isometric force on the humerus (the bone of the wing that attaches to the shoulder). These studies revealed that the SB is positioned to serve as the primary humeral depressor but, in addition, the SB can also pull the wing forward (protraction). The TB also acts as a depressor of the wing but, in contrast, is positioned to pull the wing backward (retraction; Dial et al. 1988).

Peripheral nerves consist, in part, of collections of motor nerve cell axons, those nerve cell extensions that conduct impulses from the cell body toward the muscle. The smallest func-

tional unit of neuromuscular organization as related to locomotion is the motor unit. A motor unit consists of a single neural component, the motor nerve cell (motoneuron), and the collection of muscle fibers it innervates, the muscle unit (for a review see Weeks 1989). The motoneuron cell body is located in the ventral horn of the gray matter of the spinal cord and it, along with its dendritic processes, is the site of synaptic input that determines the motoneuron's level of excitability and ultimate involvement in locomotion.

Within the vertebrate spinal cord, the cell bodies of motoneurons that send axons to a particular muscle are clustered in groups known as motor pools. Within a muscle's pool, or across pools for groups of muscles, motoneurons are selectively activated to complete a locomotor task (for a review see Burke 1981, Stuart and Enoka 1983). Thus, the anatomical segregation of motor pools within the spinal cord reflects to some degree an organization of neurons related to

function. Does such an organization exist for the SB and TB?

Some anatomically complex muscles can be divided into functional subregions (Weeks 1989). These subregions are served by axons that course through a single first-order nerve branch peripherally; the axons are traceable to motoneuron cell bodies that comprise a subset of the motor pool of the parent muscle. To determine whether the motoneurons of the SB and TB are organized as subsets within the spinal cord motor pool of the pectoralis, the anatomical tracer lectin-conjugated horseradish peroxidase (WGA-HRP) was used. WGA-HRP is one of several compounds available that are known to be actively transported by neurons exposed to it; when WGA-HRP is injected into a muscle, the axons innervating that muscle will absorb the compound, transport it toward the spinal cord, and concentrate it in the motoneuron cell bodies.

WGA-HRP was injected in various combinations into the SB and/or TB

of several anesthetized pigeons. Although these studies demonstrated overlap of the two motor pools, the SB neurons were found to be located more anteriorly in the spinal cord than the TB neurons (Sokoloff et al. 1989). The motoneurons coursing to the SB and TB are packaged into discrete anatomical units, which might reflect a functional differentiation in their use.

Finally, muscles are not necessarily homogeneous in fiber size or in their chemical and contractile properties. The relative percentage of different fiber types within a muscle is thought to reflect that muscle's functional role. Various histochemical techniques, which are an indirect approximation of fiber chemistry, can be used to identify fiber types. Weeks (1989) has outlined the procedure and noted some of its limitations.

Histochemical techniques reveal two fiber types in the pigeon pectoralis: large fibers (78.2 μm diameter), which appear to have little aerobic capacity, and small fibers (33.5 μm diameter), which are aerobic (Figure 3; George and Naik 1960, Talesara and Goldspink 1978). A systematic sampling of different portions of the SB and TB in seven pigeons revealed that, on average, the SB possesses 4% more large fibers than the TB. Given that the large fibers possess approximately a twofold greater mean diameter than the small fibers, and that force of a muscle is in proportion to the cross-sectional area of its fibers, this 4% difference may reflect a functional specialization important for the control of the wing during flight (Kaplan and Goslow 1989).

Electrical activity patterns reflect independent function between parts of the pectoralis. The above evidence for a functional partitioning of the SB and TB is, of course, primarily circumstantial. Are there ways to demonstrate *in vivo* a division of labor? Electromyography is a technique wherein fine wires are implanted in a muscle to record changes in voltage coincident with contraction-relaxation cycles. When properly amplified and displayed, the resultant electromyographic records (EMGs) can be correlated to movements, thus providing a basis on which to interpret a muscle's role in locomotion. We ob-

Figure 4. Pattern of muscle activity during flapping flight in the domestic pigeon. Arrows designate the initiation of downstroke. The electrical activity of the SB and TB begins in the middle of the upstroke, several milliseconds before the wing turns around to begin its descent. During slow flight, the SB begins activity earlier (vertical lines) than does the TB.

tained EMGs from the SB and TB of the pectoralis in adult pigeons during takeoff, level flight, and landing, and we simultaneously recorded flight behavior on 16-millimeter film (at speeds of 64–200 frames/sec). During level flight, EMG activity begins in the SB and TB before wing downstroke and ends approximately halfway through downstroke (Figure 4).

When the subtleties of limb kinematics and muscle electrical patterns are measured and correlated, two observations emerge that support a division of labor between the SB and TB. First, during slow flight (3–7 m/sec), a statistically significant difference occurs in the onset of activity of the two portions of the pectoralis (Figure 4). Second, as might be expected, both parts of the pectoralis in pigeons show the highest EMG intensities during takeoff and landing when power requirements are higher than for level flight (Figure 5). Somewhat

unexpectedly, however, we observed markedly different intensities of EMG activity from the SB and TB when we compared large-amplitude and small-amplitude wingbeats. Although electrical activity is high in both muscle portions at takeoff and landing, that in the TB often declines to near zero when wing amplitudes are small (Figure 5; Dial et al. 1987, 1988).

Future studies of the pectoralis. The data reviewed here support the hypothesis that the SB and the TB of the pectoralis of the pigeon are organized for, and are capable of, differential input to the wing during flight. From these data, however, further questions arise.

Each of the major nerves that innervate the SB and TB possess secondary branches deep within the muscle (Figure 2b). Do these secondary and tertiary nerve branches represent more finely partitioned func-

Figure 5. Wingbeat amplitude and body orientation for the three modes of flight in anterior perspective. **a.** Acceleration after release from hand, large wingbeat amplitude, body angle near horizontal. **b.** Fast flight, small wingbeat amplitude, body angle near horizontal. **c.** Landing, large wingbeat amplitude, body angle near vertical. The corresponding electrical activity of the SB and TB is shown below. The TB, the only part of the pectoralis to have a retractive component, is most active during landing. (After Dial et al. 1987.)

tional units?

The electrical activity in the SB and TB begins in the middle of the upstroke several milliseconds before the wing turns around to begin its descent (Figure 4). Because the pectoralis is active and is presumably being stretched during late upstroke, can elastic energy storage within the muscle and its connective tissue components be accumulating (see Biewener 1989)?

Because a lag exists between electrical activity and force production, when during a wingbeat is a force actually delivered to the bone of attachment? Note in Figure 3 that the large fibers tend to be found along the margin of a connective tissue boundary and enclose the small fibers to the inside. This arrangement is unusual for vertebrate muscle; large and small fibers are generally interspersed. The large difference in the size of the two types of fibers is also unusual. When are the large fibers used in flight?

Wishbone springs and air sacs: new interpretations

One major void in understanding of the control of the wing has been the inability to document the precise

movements of its skeletal elements during flight. Aspects of the aerodynamics of flight can best be studied in a situation where the conditions surrounding a flying bird are controlled. To this end, we designed and built a wind tunnel. To study the precise movements of the wing skeleton during flight, we employed a cineradiographic system that records successive x-ray images at 200 frames/sec. This apparatus could accommodate a flight chamber which was appropriate for smaller birds, but was too restricted for pigeons. Hence we began using European starlings. Our initial intent was to document the movements of the wing skeleton; we were surprised to discover that the bones of the shoulder and thorax move rhythmically also.

The wishbone of starlings is a spring. We radiographed European starlings both from the side and from above as they flew in the wind tunnel at air speeds of 9 to 20 m/sec (Figure 6). During downstroke, the shafts of the furcula (wishbone) bend laterally (Figure 1a–c, top). During the upstroke (Fig. 1d), the furcula recoils to its original resting position. The mean

increase in the distance between the dorsal ends of the furcula in four birds was 5.8 mm (SD 1.0 mm), an increase of 47% over the resting distance, which averaged 12.3 mm (SD 0.2 mm). Furcular spreading begins as the end of the humerus closest to the elbow moves forward during the upstroke-downstroke transition, before the initiation of humeral depression, and continues throughout downstroke. The dorsal ends of the strutlike coracoids (stout bones connecting the shoulder to the sternum) and the rostral ends of the scapulae, both of which are intimately bound to the furcula, are also displaced laterally.

The sternum also exhibits cyclic movement with each wingbeat. During downstroke, the sternum ascends and moves caudally; during the subsequent upstroke it descends and moves rostrally. These excursions are not simple linear displacements; they differ in their pathways and in the relative displacement of the rostral and caudal ends of the sternum (Figure 1a–d, bottom).

With the assistance of our colleagues from Harvard University, J. Harry and N. Heglund, we determined additional information about the furcula of starlings: the force required to bend fresh, excised starling furculae through their normal range of excursion is 0.6 to 0.8 N (N = newton, a unit of force equal to approximately 100 grams weight), the furcula appears to act as a slightly damped spring, and the amount of elastic energy recovered from the furcula during upstroke is negligible (Jenkins et al. 1988).

These data illustrate that the skeletal components of the shoulder and thoracic cage are dynamic during flight. Of what use are these movements to birds?

Do furcular and sternal dynamics facilitate respiration? Unlike the lungs of mammals, bird lungs are interconnected to a system of thin-walled air sacs by a complex array of tubes. Air is continuously directed through the lungs during inspiration as well as expiration. The dynamics of airflow through the bird trachea, lungs, and air sacs has challenged respiratory physiologists for many years, and the controlling mechanisms remain elu-

Figure 6. Cineradiograph of a European starling as it flies in a wind tunnel. The downstroke begins in a and ends in f.

sive (Brackenbury 1987, Kuethe 1988, Phillips et al. 1985). Current interpretations of the mechanics of avian respiration are derived primarily from observations on stationary birds and are based on the supposition that all of the air sacs are simultaneously inflated and then deflated (Figure 7; Brackenbury 1987).

Our observations raise the question whether such an interpretation is accurate for birds in flight. The shafts of the furcula lie in intimate relation to

the walls of the clavicular air sac. Through observations on both alert and anesthetized starlings, we determined that inflation of the clavicular air sacs can cause a spreading of the furcula and that, in resting starlings, positive pressure in the clavicular air sac follows compression of the posterior thoracoabdominal region. These observations are consistent with our kinematic data that demonstrate coupling between furcular spreading (presumptive inflation of the clavicular

sac) and sternal ascent and retraction (presumptive compression of the posterior air sacs; Figure 7).

Starlings do not inhale and exhale with each wingbeat as might be expected; they possess a respiratory rate during flight of about 3 HZ and a wingbeat frequency of 12–14 HZ. Our cineradiographs, however, have established that furcular and sternal movements are synchronized 1:1 with wingbeat. We hypothesize that the furcula acting as spring and the ster-

Figure 7. Skeletal movements and air sac dynamics in flight. It is proposed that as the wing is depressed during the downstroke (left to right), the furcula spreads to inflate the clavicular air sac and the sternum elevates to compress the posterior air sacs. During the subsequent upstroke, the furcula collapses medially and the sternum descends. These skeletal movements may act as a secondary respiratory pumping mechanism to move air between the air sacs and lungs during flight.

num acting as a pump might represent a secondary respiratory pumping mechanism between the air sacs and the lungs that is capable of operating independently of inhalation and exhalation and that might serve the increased metabolic demands of flight (Jenkins et al. 1988).

Further investigation. It seems reasonable to suggest that the movement of the furcula might also assist in flight by increasing the spread of the wings during downstroke to alter the mechanical advantage of the pectoralis or enhance the upstroke by springing the wing upward upon recoil. At the moment, experimental data are not available to support or refute these possibilities.

Although the furcula in starlings bends and recoils over a wide range, the clavicles of some birds may not act in this manner. Compare the starling furcula (Figure 1a) to the elongate, gracefully back-swept furcula of the pheasant, the relatively short and stout furcula of a hawk, and the slender, almost delicate, furcula of a parrot (Figure 8). The structural diversity of avian furculae that is seen in different species may vary with body size, wingbeat frequency, or flight mode.

Finally, what might the furcula's function have been in the earliest birds? The Jurassic bird *Archae-*

opteryx is known from six specimens. Examination of the furcula in the London specimen reveals that its greatest cross-sectional area is aligned transversely, so it would probably resist bending (Figure 9). We can speculate, therefore, that the furcula of the earliest birds did not act as a spring but may have served as a strut or brace.

Conclusions

The evolution of flapping flight in birds is recognized as a key historical event that contributed to the group's biological success. As a result, there is much interest in the origin of flight and its subsequent radiation. These problems are complex, however, and viewpoints differ (Bock 1969, Hecht et al. 1985, Padian 1986). Many neuromuscular and musculoskeletal correlates to flight are still undiscovered. Like Leonardo da Vinci in his pursuit of artificial flight, we plan to continue our studies of the flight mechanisms of modern species. Only through such studies can we hope to provide a reasonable reconstruction of the evolution of this most amazing and successful form of locomotion.

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Figure 8. Diversity of shoulder girdles among birds. Among modern flying birds, the shoulder girdle varies considerably relative to the size and shape of the bony elements. The furcula may be back-swept and slender (pheasant, *Phasianus colchis*), short and stout (hawk, *Buteo buteo*), or slight (parrot, *Ara macao*).

Figure 9. The London specimen of *Archaeopteryx lithographica* (left) from the Jurassic beds of the Solnhofen limestone (Germany). The robust furcula (right) is shaped somewhat like a boomerang, which precludes its function as a spring. The furcula probably functioned as a strut or brace for the shoulder in early birds.

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