

# A FUNCTIONAL ANALYSIS OF THE PRIMARY UPSTROKE AND DOWNSTROKE MUSCLES IN THE DOMESTIC PIGEON (*COLUMBA LIVIA*) DURING FLIGHT

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## SUMMARY

In domestic pigeons (*Columba livia*), the electrical activity of the major depressor muscle of the wing, the pectoralis (pars thoracicus), begins in late upstroke well before the wing begins its downstroke excursion. The two architecturally distinct heads of the pectoralis, the sternobrachialis and the thoracobrachialis, are differentially recruited during take-off, level flight and landing. In addition to wing depression, the sternobrachialis protracts the humerus and the thoracobrachialis retracts the humerus. At the point of transition from wing upstroke to downstroke, the pectoralis EMG signal typically exhibits a reduction in amplitude. The supracoracoideus, in addition to an expected EMG associated with wing elevation, is co-activated with the pectoralis about 50% of the time.

## INTRODUCTION

The pectoralis and supracoracoideus muscles of birds are often regarded as simple elevators and depressors of the wing during flight. The avian pectoralis, however, is architecturally complex and, unlike any other tetrapod muscle, may constitute up to 35% of total body weight. The supracoracoideus is a highly derived muscle as reflected by its anatomical location; the muscle's belly lies deep to the pectoralis and below the glenohumeral joint, but its tendon inserts on the dorsal aspect of the humerus. Our understanding of the functional contribution of these muscles to flight has been based primarily on studies of their structure at gross and microscopic levels.

Previously available data on the pigeon pectoralis have been reported from studies directed at other aspects of flight. Butler, West & Jones (1977), in an investigation of

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respiratory and cardiovascular responses during sustained flight, showed that pectoralis activity varies with behaviour (i.e. take-off, level flight and landing). Aulie (1972) demonstrated that there is no consistent coordination between pectoralis activity and heart rate in pigeons. Data from other birds confirm the existence of modulation in the activity of the pectoralis. Hagiwara, Chichibu & Simpson (1968), in a study of three species of hummingbirds and one species of finch, reported that the pectoralis contraction is a 'twitch' per wingbeat during hovering flight in the hummingbirds, becomes a brief 'tetanus' during forward flight, and that the contraction time is correlated with a relatively constant wingbeat frequency in all four species. Aulie (1970) obtained similar results from budgerigars flying in a wind tunnel. During normal flight, the pectoralis performed twitch contractions at a relatively constant frequency and brief tetanic contractions during strenuous flight. EMG amplitude was lowest at a flight speed of  $35 \text{ km h}^{-1}$  and increased at both lower and higher speeds. Finally, in a wind tunnel study of the herring gull, Goldspink, Mills & Schmidt-Nielsen (1978) reported that EMGs from the pectoralis during flight diminished to low amplitude in gliding.

This study, based on kinematic and EMG analysis, defines more precisely the activity patterns of the pectoralis with respect to the wingbeat cycle, and provides evidence of both the structural and functional complexity of this muscle. In addition, we present EMG data from the major elevator of the wing, the supracoracoideus, about which little has been previously known.

#### MATERIALS AND METHODS

Experiments were performed on 13 wild type pigeons (*Columba livia*) with a mean body mass of 355 g (s.d. = 30). Ten birds were surgically implanted for electromyography; three additional birds were used for acute experiments on the contractile properties of muscle. Birds were trained to fly approximately 35 m down a hallway to a landing perch. Each bird underwent a training regimen that consisted of flying with a weighted harness (40 g) until it was capable of maintaining level or ascending flight along the entire flight course. Pigeons were maintained in an outdoor aviary and were supplied with pigeon mix and water *ad libitum*.

#### *Cinematography*

Simultaneous cinematography was conducted for each EMG sequence analysed. Two 16 mm cameras (Hi-Cam, Red Lakes Lab.,  $200 \text{ frames s}^{-1}$ ; Bolex H16,  $64 \text{ frames s}^{-1}$ ), electrically coupled to an FM tape recorder, provided for analysis of wing position coincident with EMG activity. The faster camera was positioned in front of the flight path (allowing determination of the upstroke and downstroke transition), and the other lateral to the flight path (providing measurements for flight speed and trajectory).

Flight velocity, body angle and changes in flight trajectory were determined from lateral projection films (which included a background grid of 10 cm squares) viewed

on a photo-optical digitizer (L-W International). Frontal projection film was used to relate wing kinematics to EMG activity.

#### *Electromyography*

Birds were initially administered intramuscular doses of ketamine ( $25 \text{ mg kg}^{-1}$ ) and xylazine ( $2 \text{ mg kg}^{-1}$ ) to induce deep anaesthesia for the surgical procedures. Supplemental amounts were given as needed. Feathers were removed around each of three skin incisions made dorsally between the scapulae, ventrally along the length of the carina in the median sagittal plane, and anteriorly at the shoulder. Electrode wires were threaded subcutaneously from their site of implantation to the dorsal incision by guiding them through a temporarily inserted polyethylene canula. Birds prepared for electromyography were given  $10\,000 \text{ units kg}^{-1}$  of penicillin daily postoperatively. All birds were able to fly in 1 or 2 days following surgery.

Birds were surgically implanted with conventional chronic bipolar electrodes (Betts, Smith, Edgerton & Collatos, 1976; O'Donovan, Pinter, Dum & Burke, 1982). A connector (9-pin Amphenol) was constructed with four pairs of electrode wires and one ground wire. Two electrode configurations and implantations were employed. (1) Paired, Teflon-coated, 18-stranded, stainless steel wires ( $0.28 \text{ mm}$  diameter, Cooner Co., Chatsworth, CA). In the middle of each wire, a  $0.5 \text{ mm}$  section of insulation was removed from its side under a binocular microscope with the aid of a small cauterizer. Each pair of etches was subsequently cleaned with a no. 15 scalpel. The insulation that remained provided for an inter-electrode distance of  $0.5 \text{ mm}$ . With a cutting needle, the paired wires were threaded through the muscle until the recording surfaces were deeply implanted. The two wires were secured upon entry and exit to prevent their movement over the course of the experiment (Mangun, Mulkey, Young & Goslow, 1986). One end of the exposed wires was sealed by stretching the insulation over the tips; the other end was connected to an Amphenol connector. (2) The second electrode design was that of Basmajian & Stecko (1962) in which bipolar silver electrodes ( $100 \mu\text{m}$  diameter,  $0.5 \text{ mm}$  surface exposure,  $0.5 \text{ mm}$  intertip distance) were surgically implanted with the aid of a 26 gauge hypodermic needle. Prior to insertion, the wires were tightly twisted with a power drill (Gorniack, 1977). The wire leaving the muscle was coiled, then stitched to available fascia to prevent movement. Following the recording session, the animal was killed (injected with FP-3 euthanasia solution) and electrode placement verified by dissection.

Two EMG recording techniques were employed: telemetry and direct wire. The telemetry technique has been described elsewhere (Chan, Rasmussen & Goslow, 1977). A cloth body harness with elastic straps to hold two transmitters (Narco-Bio, 18 g each) was placed high on the animal's back near its centre of gravity. Transmitters were positioned so as not to obstruct the bird's upstroke. The electrical signal from the muscle was received by a frequency-modulated radiowave receiver (Narco-Bio), amplified (Grass P511), and stored on FM tape (Hewlett-Packard 3694A) at  $38 \text{ cm s}^{-1}$ . For analysis, signals were played back at  $38$  or  $81 \text{ cm s}^{-1}$  through a bandpass filter (Universal, 1952, cut-off frequencies of  $4 \text{ Hz}$  and

2000 Hz) and displayed (Hewlett-Packard 7402A chart recorder, frequency response 40 Hz).

The second recording method involved wiring the animal directly to the preamplifiers using 18 m of lightweight, shielded cable conductor (NMUF 4130-4046SJ, Cooner Wire Co., Chatsworth, CA). The shield was used as a ground. The cable was connected to the Amphenol plug and taped to the flank of the bird to minimize obstruction during flight. Up to four electrode sets were surgically placed into each bird, but regardless of the recording method, only two sets were monitored at any one time.

Two pairs of electrodes were implanted within 5 mm of one another in two birds (one pair in the sternobrachialis and one pair in the supracoracoideus) to evaluate the effect of different electrode positions within the region of the muscle utilized in these experiments. No significant difference (Student's paired *t*-test) in onset and offset times was found from adjacent electrodes in either pigeon.

#### *Cross-talk*

Our EMG electrodes were designed to record selectively from discrete regions within a muscle. Nevertheless, the potential exists for detection of electrical activity from adjacent muscles or muscle compartments (Mangun *et al.* 1986). We were concerned about volume-conducted EMGs from the sternobrachialis (SB) and thoracobrachialis (TB) to the supracoracoideus, and from SB to TB. We tested for this cross-talk in two ways.

In one set of experiments, cross-talk to the supracoracoideus from the two heads of the pectoralis was measured for both EMG electrode types in four acute experiments following the procedure of Zajac (1985). Subsequent to flight sequences in which EMGs were recorded, each bird was deeply anaesthetized and the nerves to the SB and TB were exposed. Supra-maximal stimulation (0.1 ms duration) of the SB or TB nerves produced an EMG potential which was detected by the indwelling electrodes. Usually, some measurable volume-conducted EMGs were also detected within the SC EMG electrode set, but the magnitude varied with electrode configuration and placement. In all cases, the extent of cross-talk was greatest for the stranded stainless steel electrodes. This procedure verified that volume-conducted cross-talk between the pectoralis and supracoracoideus electrodes is possible. In the data presented here from flight experiments, however, consistent differences in the offset and onset times of the two muscles were taken as evidence that the signals were not significantly mixed.

A second set of denervation experiments was designed to determine the extent of cross-talk between silver electrode sets within the SB and TB heads. In two birds electrodes were surgically implanted into each head as described above, and EMGs during flight were monitored. Each bird was subsequently anaesthetized, and the nerve to either the SB or TB sectioned. Upon recovery (within 20 h), the bird was able to fly (although somewhat laboriously), and EMGs were monitored from the denervated as well as innervated heads (Fig. 1). The data reveal little significant intramuscular cross-talk between silver electrode sets within the pectoralis.

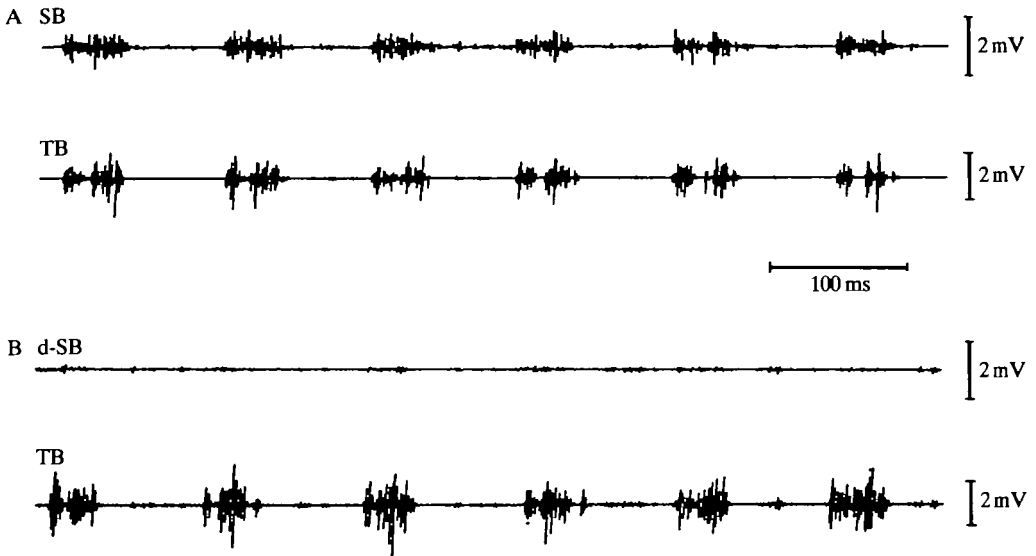


Fig. 1. Muscle denervation experiment designed to determine the recording selectivity of silver electrode sets. EMG activity from the sternobrachialis (SB) and thoracobrachialis (TB) of the pectoralis during flapping flight was measured by surgically implanted bipolar silver electrodes ( $100\ \mu\text{m}$  diameter;  $0.5\ \text{mm}$  surface exposure;  $0.5\ \text{mm}$  intertip distance). (A) Normal electrical activity of the two heads; (B) electrical activity 20 h after the SB had been denervated (d) by surgical resection of its nerve. The increased amplitude of the TB EMG relative to its pre-denervation amplitude probably reflects compensatory activity of this head. For a second bird (TB denervated), pre- and post-denervation records were similar to those shown. The amount of intramuscular EMG cross-talk was judged negligible.

We believe that the signals presented in this report represent accurately the EMG activity of the implanted muscles.

#### *Mechanical properties*

The actions and contraction times of the supracoracoideus and the SB and TB heads of the pectoralis were studied in three birds. The birds were anaesthetized and intubated *via* the trachea after the posterior abdominal air sacs had been surgically opened to establish a unidirectional flow. A mixture of humidified nitrogen (70%), oxygen (30%) and carbon dioxide (<1%) maintained at  $40^\circ\text{C}$  was passed continuously over the lungs.

Nerves were isolated with minimal disturbance to the muscle's blood supply, wrapped by a silver electrode and subsequently sheathed by cannula tubing to minimize desiccation and current spread. Exposed muscles were bathed with warm mineral oil. A  $40^\circ\text{C}$  muscle temperature was maintained with the aid of a heat lamp. The nerve that innervates the coracobrachialis caudalis accompanies the main trunk of the brachial plexus that gives rise to the two pectoral nerves. To eliminate any

possible influence by the coracobrachialis caudalis on humeral movement, this muscle was bisected.

To measure the forces generated by the SB and TB, a force transducer was used to sense the moment of isometric force developed at the distal humerus during repetitive supra-maximal stimulation (100 Hz, 0.1–0.2 ms pulse duration) of the individual nerves. A short piece of surgical silk (compliance  $0.45 \mu\text{m kg}^{-1} \text{cm}^{-1}$ ), tied around the distal humerus, was attached to the transducer which was placed in three positions to measure the approximate components of depression, protraction and retraction. Force measurements were made with the humerus set at two different angles to duplicate its approximate position at the initial and middle stages of wing downstroke.

## RESULTS

### *Myology*

The general arrangement of the pectoralis and supracoracoideus is given by George & Berger (1966). Only certain features necessary for functional interpretation are noted here. We employ the nomenclature set forth in *Nomina Anatomica Avium* (Baumel *et al.* 1979).

#### *M. pectoralis pars thoracicus*

Although minor components of the pectoralis exist in pigeons, the pars thoracicus (Fig. 2) is by far the largest component and represents the major depressor of the

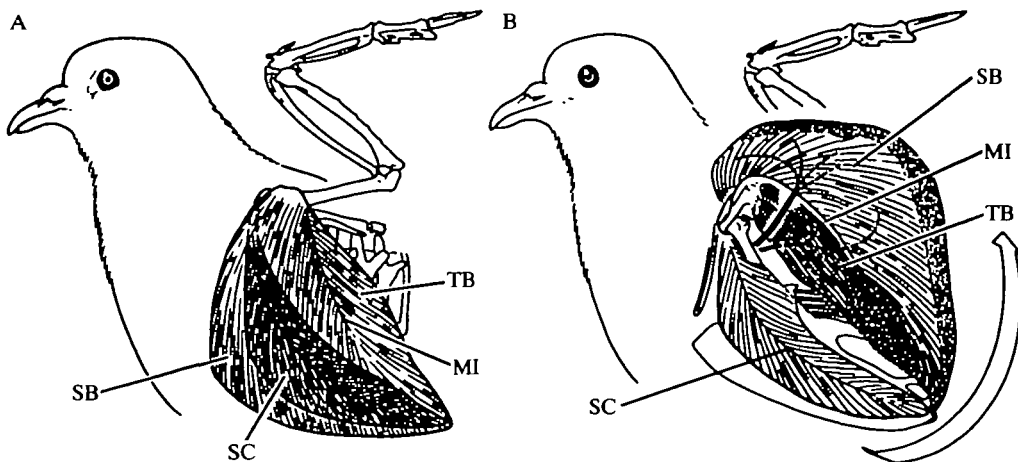


Fig. 2. Anatomy of the pectoralis muscle in *Columba livia*. (A) Lateral view of the *M. pectoralis* (pars thoracicus) to illustrate the division of the sternobrachialis (SB) and the thoracobrachialis (TB) heads by a fascial plate, the membrana intramuscularis (MI). The ventrally positioned *M. supracoracoideus* (SC), the primary wing elevator, lies deep to the pectoralis against the sternum. (B) Deep view of the pectoralis (reflected). Note the innervation of the SB and TB regions by distinct branches of the brachial plexus. The anterior nerve innervates the SB, the posterior nerve the TB.

wing (George & Berger, 1966; Raikow, 1985). A fascial plate (*membrana intramuscularis*) is continuous with the main tendon of the pectoralis and divides the muscle into two heads, the sternobrachialis (SB) and the thoracobrachialis (TB) (Fig. 2A,B). These two heads possess separate origins and fibre orientations. Furthermore, Kaplan (1987) demonstrated that each is innervated by distinct branches of the brachial plexus (Fig. 2B).

The fascicles of the SB originate on the anterolateral surface of the clavicle, along the entire sternal carina, and from the body of the sternum lateral to the supracoracoideus. These fascicles, primarily oriented dorsoventrally, insert into the lateral surface of the intramuscular membrane and also directly on the cranial surface of the deltopectoral crest of the humerus. The TB, in contrast, arises for the most part from the posterolateral surface of the sternum, as well as from the lateral trabecula and membrane of the lateral notch (Raikow, 1985). The fascicles of the ventral part of the TB insert on the medial aspect of the intramuscular membrane; the more dorsal fibres converge on a separate tendon that joins the main tendon of the pectoralis close to its insertion into the deltopectoral crest. The fascicles of both TB components are oriented primarily horizontally.

### *M. supracoracoideus*

This muscle lies deep to the pectoralis pars thoracicus (primarily the SB) and is the primary elevator of the wing (Fig. 2A,B). Its fascicles arise from the dorsal half of the carina, the adjacent body of the sternum, and a small area on the base of the coracoclavicular membrane. The tendon of insertion passes dorsally through the triosseal canal to insert on the dorsal surface of the proximal humerus.

### *Kinematics*

Detailed accounts of the wing movements of pigeons during take-off (Simpson, 1983) and various kinds of flapping flight (Brown, 1953, 1963; Pennycuik, 1968*a,b*) are available and present similar conclusions. The two basic phases of flapping flight are a downstroke phase, when the wing is brought downwards and forwards to provide power and lift, and a complicated upstroke phase that prepares the wing for the subsequent downstroke (Fig. 3). We present only a generalized chronological description of the wingbeat cycle. We have adopted the terminology of Simpson (1983) for the phases.

At the beginning of downstroke, the humerus is abducted to a nearly vertical position. The humerus is also retracted and, as seen in lateral view, projects backwards to form an obtuse angle of about 120° with the body axis. The elbow and wrist joints are fully extended. During the first half of the downstroke, vertical downstroke, the humerus adducts to bring the wing into a horizontal position. At the same time, the humerus may pronate (to drop the leading edge relative to the trailing edge) and protract slightly, but we could not resolve these subtleties from our films. During the second half of downstroke, or forward swing phase, the wings move downwards and forwards until they lie parallel to and in front of the body. This is

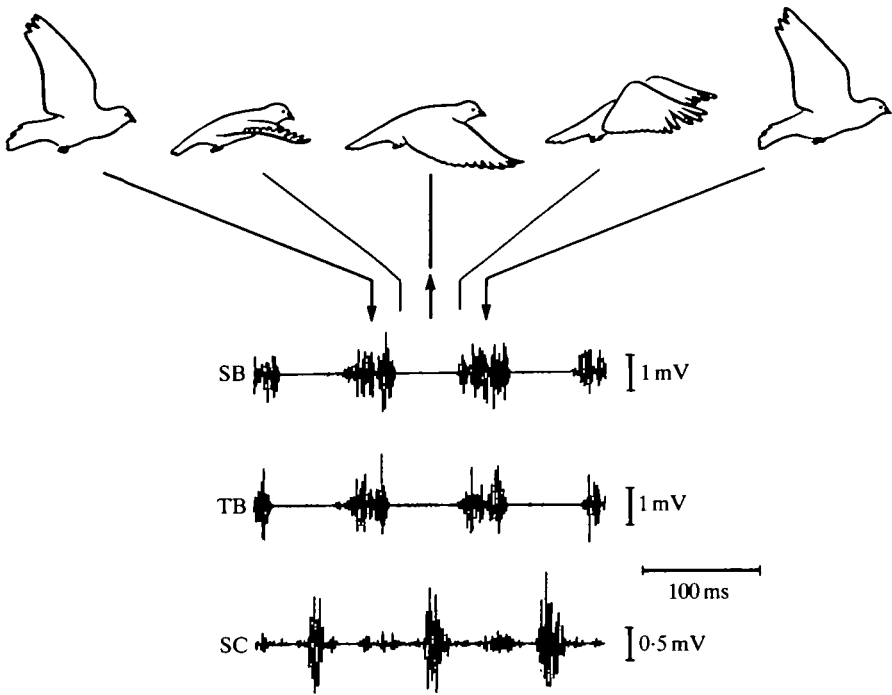


Fig. 3. Pattern of muscle activity during flapping flight. Arrows designate the initiation of downstroke (downward arrow) and of upstroke (upward arrow). SB, sternobranchialis head of the pectoralis; TB, thoracobranchialis head of the pectoralis; SC, supracoracoideus. Maximum flight speed, attained at level flight, was  $12 \text{ m s}^{-1}$ .

accomplished in part by protraction of the humerus ( $15\text{--}20^\circ$ ) as it adducts  $40\text{--}50^\circ$ . The wrist and elbow remain extended.

Upstroke can be subdivided into three phases; however, we do not wish to imply that these phases are functionally discrete. The first third of the upstroke, a transitional phase, is marked by a reversal of the humeral movement that occurs in the forward swing phase, and flexion of the elbow and wrist. Backward flick follows the transitional phase. The humerus is rapidly retracted and abducted (elevated) while the elbow and wrist remain flexed. The last phase of upstroke, preparatory to downstroke, is characterized by wing extension. The humerus protracts a few degrees and is abducted fully; extension at the elbow and wrist is evident.

### *Electromyography*

#### *General patterns*

The EMG activity patterns for a flapping bird in level flight ( $8 \text{ m s}^{-1}$ ) are presented with reference to a typical wingbeat cycle (Fig. 3). Electromyographic data were derived from flight speeds which varied from  $3$  to  $12 \text{ m s}^{-1}$  and wingbeat frequencies of  $7\text{--}10 \text{ Hz}$  (Fig. 4). To compare statistically the onset and offset times of EMG signals, wingbeat cycles were normalized to  $100\%$ , with the beginning of



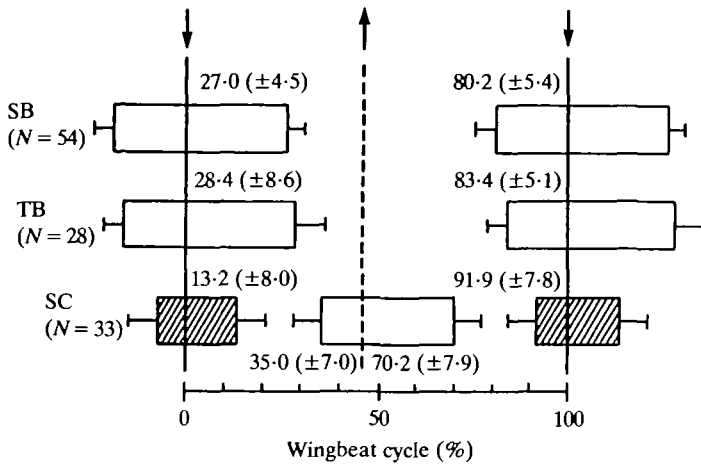


Fig. 4. Summary of the muscle activity during flapping flight for 10 pigeons (flying at  $3\text{--}12\text{ m s}^{-1}$ ). Wing beat cycles were normalized to 100%, with the beginning of the downstroke represented as zero and the end of the upstroke as 100%. Arrows designate the onset of downstroke (downward arrow) and upstroke (upward arrow). The bars represent the average period of continuous activity for each muscle. Values for the mean onset of activity are expressed as a percentage of the wingbeat cycle. A standard deviation is shown by superimposed lines at the ends of the bars. Note EMG activity of the sternobrachialis (SB) and thoracobrachialis (TB) heads of the pectoralis prior to the commencement of downstroke and of the supracoracoideus (SC) prior to upstroke. Also, note the frequency of double bursts generated from the SC. *N*, sample size of wingbeats analysed. Cross-hatching represents muscle activity that occurred in approximately 50% of observations.

downstroke represented as zero and the end of the upstroke as 100%. The duration of the upstroke and downstroke are essentially equal.

Electrical activity of both pectoralis heads begins in the preparatory phase of upstroke. Over the range of flight speeds, this onset occurs *prior* to downstroke at 80.2% of the wingbeat cycle for the SB, and at 83.4% of the wingbeat cycle for the TB (Fig. 4). Activity continues in both heads until the wing reaches the transitional position between vertical downstroke and forward swing.

Electrical activity in the supracoracoideus is often biphasic. The activity begins on average 35% into the wingbeat cycle, coincident with forward swing of the downstroke. This onset occurs on average 10% of a wingbeat cycle *prior* to upstroke (Fig. 4). The burst ends 70% into the flap cycle in association with the backward flick of upstroke. A smaller second burst, which occurred in 48% of our recordings, begins in late upstroke and continues into vertical downstroke. This activity overlaps that of the pectoralis and represents co-activation of antagonistic muscles. The double burst pattern is variable; in some cases it appears and then disappears within a single flight sequence, whereas in others it is consistently present (Fig. 3) or absent. No relationship of the double burst to flight speed, body angle or wingbeat amplitude was evident.

### *Differential activity in SB and TB*

The two heads of the pectoralis can be activated independently during take-off, flapping flight and landing. Two sets of observations support this conclusion. First, simultaneous recordings from each head reveal differences in activity onset times. In slow flight sequences ( $3\text{--}5\text{ m s}^{-1}$ ) in two birds, SB activity commenced on average  $12.2\text{ ms}$  ( $N = 42$ ) prior to TB. In fast flight sequences ( $7\text{--}12\text{ m s}^{-1}$ ) in six birds, however, activity ( $N = 24$ ) of the two heads was synchronous. Second, the SB showed greatest spike amplitude during take-off and landing and significant diminution during fast, level flight, whereas the TB exhibited moderate EMG activity during take-off, little activity during fast and level flight, and its relatively greatest amplitude during landing (Fig. 5).

### *Patterns of EMG signals*

The pattern of spikes representing each burst of electrical activity within the two pectoralis heads during flapping flight usually has two characteristic features: (1) an abrupt, large amplitude onset and (2) a brief diminution or interruption of activity

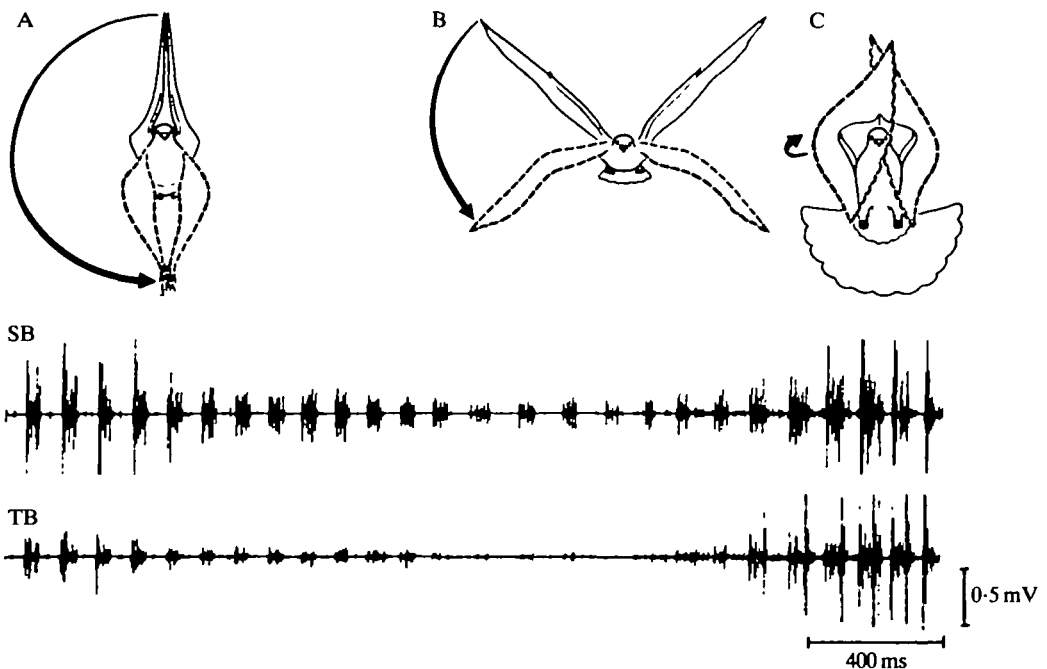


Fig. 5. Electrical activity of the sternobrachialis (SB) and thoracobrachialis (TB) at release from the hand (A), during high to low amplitude flapping (B), and during landing (C). Large amplitude spikes are evident in both subregions early and late in the sequence; however, note the importance of the TB during landing when the pigeon's trunk is oriented in a near vertical position. Silhouettes of the birds illustrate wingbeat excursion and trunk orientation with corresponding EMG spike amplitudes (after Dial, Kaplan, Goslow & Jenkins, 1987).

within the burst at the upstroke–downstroke transition. Each has implications for motor control and will be considered in turn.

The rapid onset of high amplitude signals may occur consistently in successive wingbeats in both heads or the pattern may vary. For example, for the SB in Fig. 3, compare the spindle-shaped burst at the beginning of the illustrated wingbeat cycle with the abrupt, high amplitude bursts that begin the next two cycles. Note also the abrupt, large amplitude onset of the supracoracoideus.

A brief, mid-burst diminution in activity within the SB and TB heads at the upstroke–downstroke transition was seen to some degree in all experiments. In some flapping sequences, the break in the continuity of the signal was consistently present (TB, Fig. 1A); in others, it was intermittent or obscure. The onset of this break occurred from 20–25 ms after the burst began and its duration was approximately 10 ms.

#### *Joint force experiments*

The SB and TB both depress the wing, but their contributions are unequal. In one experiment, for example, at the beginning of downstroke isometric forces were 12.5 N for the SB and 6.1 N for the TB. In the mid-downstroke position (equivalent to the beginning of the forward swing phase), the depressive forces were 6.3 N and 3.7 N, respectively (Fig. 6). Of the total depressive force produced, the SB produced 67 % initially and 63 % at mid-downstroke. The maximal forces generated by *in vivo* stimulation of the nerves to the SB and TB cannot be assumed to duplicate those of a bird in flight. They do, however, provide a means to compare each muscle's potential contribution to the movements of the wing.

Relative to the TB, the SB is more favourably positioned to produce humeral protraction. In the mid-downstroke position (equivalent to the beginning of the forward swing phase), the SB produced 100 % of wing protraction (3.5 N). The TB, in contrast, is more favourably positioned to produce humeral retraction and contributes 100 % of this total force at both wing positions. It should be noted that this retraction force may be particularly large at the beginning of forward swing (4.7 N).

#### DISCUSSION

EMG activity in the pectoralis and supracoracoideus invariably occurs *prior* to wing downstroke and upstroke, respectively. A similar pattern of electrical activity has been reported in the pectoralis from two genera of bats (*Antrozous* and *Artibeus*; Hermanson & Altenbach, 1981, 1985). Additionally, Aulie (1972) noted 'a series of four to ten muscle potentials' in the pigeon pectoralis prior to downstroke. Elsewhere (Dial, Kaplan, Goslow & Jenkins, 1987) we have considered that this activity in pigeons represents stretching of the muscle under active tension, a phenomenon not uncommon in the limb muscles of terrestrial vertebrates (Alexander, 1984) which relates to the energetics of locomotion (Cavagna, Heglund & Taylor, 1977).

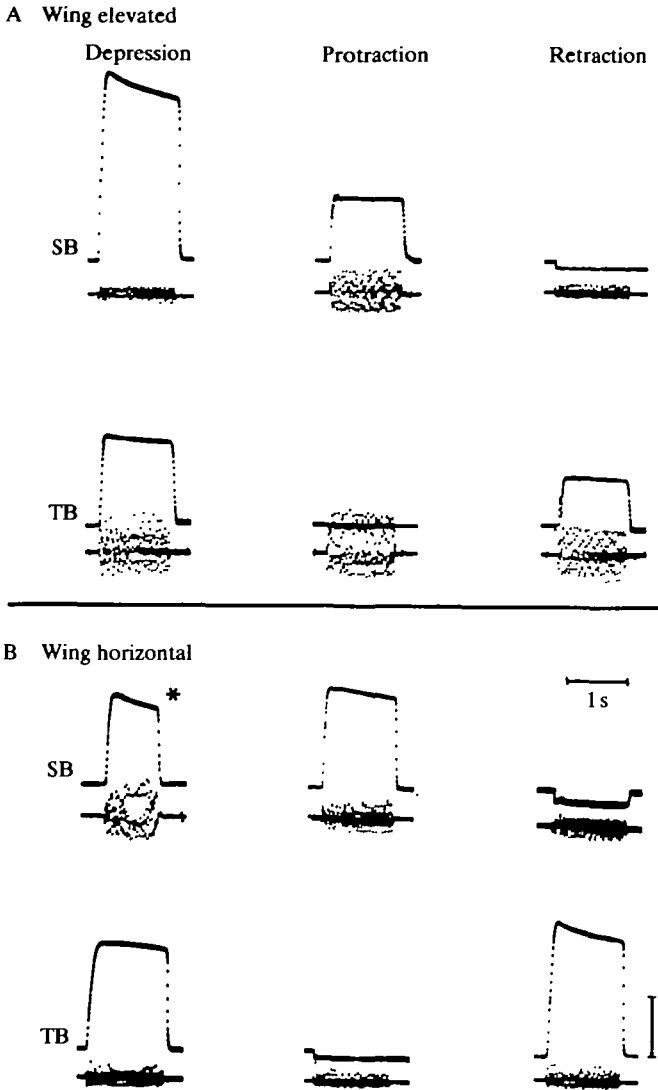


Fig. 6. Isometric measurements of depressive, protractive and retractive forces acting on the humerus during repetitive stimulation of the nerves to the sternobrachialis (SB) and thoracobrachialis (TB). EMG activity from indwelling, fine-wire electrodes is shown below each force trace. The three measurements were made with the humerus in one of two positions. (A) Wing fully elevated in a position equivalent to the beginning of vertical downstroke. Humerus-to-horizontal angle =  $80^\circ$ ; humerus retracted to form an angle of  $60^\circ$  with the median sagittal plane. (B) Wing horizontal in a position equivalent to mid-downstroke or the beginning of forward swing. Humerus-to-horizontal angle =  $0^\circ$ ; humerus retracted to form an angle of  $60^\circ$  with the median sagittal plane. Force bar, 2 N, except at \* where bar is 4 N.

In flight sequences where wingbeat amplitude varied (e.g. Fig. 5), a corresponding positive relationship with EMG activity (i.e. spike amplitude and number) was apparent. Although an absolute correlation of EMG activity with force output may be spurious, it has been shown elsewhere that gross changes in pectoralis EMG activity vary predictably with flight speed (Aulie, 1970), oxygen consumption (Butler *et al.* 1977) and wing loading (Goldspink *et al.* 1978). Quantitative measurements of simultaneous EMG activity and force development are necessary to better understand this relationship.

We provide evidence for partitioning of activity between two parts of the pectoralis. As a change in body attitude is accompanied by a corresponding change in wing excursion, we believe that subdivisions of the pectoralis modify their influence on humeral movement. Our conclusion is based on the following observed differences in the two heads: (1) the orientation of the muscle fascicles; (2) the sites of origin and insertion; (3) the distinctive patterns of EMG activity during different modes of flight; and (4) results from 'muscle force-nerve stimulation' experiments. The SB is considered to be the primary humeral depressor and assists in protraction, while the TB complements the SB in depression but assists in retraction of the humerus. Evidence presented in this study suggests that the TB is particularly important during landing, and perhaps hovering (see Pennycuick, 1968*b*) when the body attitude approaches vertical and the wings thrust backwards and downwards to reduce flight speed. In contrast, the SB is apparently important in all modes of flight.

The functional significance of the double burst pattern observed in the supracoracoideus is not clear. Co-activation of antagonistic muscles that stabilize a common joint is consistent with current theory of neural control. However, the biphasic pattern of the pigeon supracoracoideus may represent a more general principle regarding the evolution of neuromuscular and musculoskeletal design of vertebrate locomotor systems. Curiously, a similar biphasic pattern has been observed in homologous muscles in other vertebrates of diverse locomotor styles. EMG activity during both swing and propulsion phases was exhibited by the supracoracoideus in *Varanus* (Jenkins & Goslow, 1983) and a similar biphasic pattern was observed in the supra- and infraspinatus in *Didelphis* (Jenkins & Weijs, 1979), *Felis* (English, 1978), *Antrozous* (Hermanson & Altenbach, 1981) and in the supraspinatus of *Canis* (Goslow *et al.* 1981). The burst associated with the propulsive phase of limb movement is most intense in terrestrial forms, whereas the upstroke burst is of higher amplitude in pigeons. One interpretation of these data is that during tetrapod evolution a conservative 'motor pattern' driving the musculoskeletal system of the shoulder has been retained. In derived forms such as birds and mammals, however, different parts of the pattern predominate. Thus, in mammals the homologues of the supracoracoideus primarily stabilize the glenohumeral joint during the *propulsive* phase, whereas in birds the supracoracoideus elevates the humerus in the upstroke which is equivalent to the *swing* phase. Evidence for conservation of motor patterns is present in the feeding system of select fish species during the evolution of trophic specialization (Lauder, 1983), and in the ontogeny of the feeding mechanism of salamanders (Lauder & Shaffer, 1986).

The diminution in the electrical activity of either the SB or TB is similar in profile to the 'silent period' that appears in the EMG of contracting muscles that are unexpectedly unloaded, or to the 'inhibitory response' that occurs when a contracting muscle is unexpectedly loaded (for a review, see Prochazka, Schofield, Westerman & Ziccone, 1977). In contrast, however, the pectoralis during normal flapping flight is not subjected to any unexpected perturbation. The secondary (smaller) EMG burst of the supracoracoideus that occurs with a pectoralis burst is not unlike the pattern observed for agonist and antagonistic muscles during ballistic movements in other vertebrates (for a review, see Ghez & Martin, 1982; Hannaford & Stark, 1985). In such movements, the agonist muscle is activated first and produces the torque required to accelerate the limb. The antagonistic muscle, which subsequently activates during the dynamic phase of movement, is thought to assist in segment deceleration and is associated with a transient silent period in the agonist EMG. The functional significance of the second agonistic burst is unknown. The pause itself could be mediated by a combination of factors of supraspinal or peripheral origin. In birds, autogenetic inhibition of the pectoralis as the muscle actively lengthens to decelerate the wing in late upswing, or stretch-evoked activity of afferents from other muscle (and possibly joint) receptors of the wing, are two possibilities of peripheral regulation.

Hagiwara *et al.* (1968) and Aulie (1970) studied EMGs of the pectoralis during flight in five relatively small species of birds and concluded that a synchronous activation of motor units during recruitment occurs to meet demands for increased force. The abrupt, high-amplitude onset of activity and the intra-burst pause in the pectoralis EMG of pigeons in flight also suggest a synchronous onset of multiple units. The intra-burst pause may reflect a 'reset' of units activated for vertical downstroke.

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