AIRFLOW SENSORS IN THE AVIAN WING

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Summary

Mechanoreceptors on or near feather follicles in the wings of birds may provide information about airflow over the wing. We studied discharge characteristics of rapidly and slowly adapting mechanoreceptors associated with propatagial covert feathers, slowly adapting receptors within the alular joint and vibration-sensitive receptors of filoplume follicles attached to the follicles of secondary flight feathers during manual feather movements and during airflow over the wing. Dorsal elevation of covert feathers produced an increase in discharge frequency related to the angle of elevation. Extension of the alula produced an increase in discharge frequency related to the angle of extension. Stimulation of receptors located on the distal half of the follicles of secondary flight feathers by airflow over the wing produced a continuous discharge whose frequency correlated with airflow velocity. There is thus abundant sensory input from the wing to the central nervous system. We conclude that birds have the necessary sensor-feather mechanisms in the wing (1) to detect an imminent stall and the location of the separation point of the airflow from the wing’s surface, and (2) to measure airspeed by detecting the frequency of vibration of the secondary flight feathers.

Introduction

Although birds’ feathers have no inherent sensory capabilities, their follicles are surrounded by a variety of mechanoreceptors with various response characteristics (Dorward, 1970; Schwartzkopff, 1973; Necker, 1983, 1985b; Gottschaldt, 1985; Hörster, 1990a,b) and structures (Stammer, 1961; Cobb and Bennett, 1970; Gottschaldt, 1985; Hörster, 1990a). Airflow directed at the feathers of the head, neck and breast of birds (Gewecke and Woike, 1978; Bilo and Bilo, 1983; Bilo et al. 1985), and at hairs on the head and antennae of insects (Weis-Fogh, 1949; Gewecke, 1974; Möhl, 1989), influences the locomotor behavior of these animals. Necker (1985a) and Hörster (1990a,b) have suggested that neural receptors associated with wing feathers might play a role in the control of bird flight.

Wing feathers are constantly exposed to airflow during flight, and their movement or vibration could stimulate mechanoreceptors associated with their follicles. We hypothesized that such sensory mechanisms detect information concerning airflow

Key words: feathers, mechanoreceptors, flight, birds, stall, airspeed, filoplumes, sensory, chicken, Gallus domesticus.
velocity and the separation of the airflow from the surface of the wing, i.e. stall. We recorded the discharge characteristics of these receptors during manual feather displacement and during various speeds and directions of an artificial airflow over the wing.

**Materials and methods**

Eleven adult, female, single-comb, white leghorn chickens (*Gallus domesticus*) purchased from a commercial source were used in these experiments. Feed was withheld from the birds overnight prior to experimentation. Each bird was killed following the experiment by an overdose of phenobarbital sodium. These experiments comply with all relevant US regulations concerning such work, and were approved by the Animal Use Committee of Kansas State University.

**Animal preparation**

Each bird was restrained in dorsal recumbency, and a local anesthetic (1% Lidocaine HCl) was infiltrated into the soft tissues of the right ventral brachium. The ulnar vein was cannulated with PE50 tubing, and an initial dose of phenobarbital sodium (75mgkg⁻¹) was given over approximately 10min, followed by smaller doses as needed to achieve a plane of anesthesia in which noxious stimuli applied to the comb of the bird produced no response (Fedde, 1977). The brachial artery was cannulated (PE50 tubing) and arterial blood pressure was monitored with a pressure transducer (model P23Db, Statham) and multichannel pen recorder (model 481, Gould Electronics). Feathers were removed from the neck, the proximal half of the left brachium and both sides of the body wall cranial to the leg.

The trachea was cannulated in the ventral mid-cervical region. Bilateral incisions between the most caudal sternal ribs allowed placement of perforated silastic tubing (5mm i.d.) into the conjoined abdominal, caudal thoracic and cranial thoracic air sacs. Unidirectional ventilation was maintained using 1 l min⁻¹ of 95% O₂+5% CO₂ that had been bubbled through heated distilled water before entering the tracheal cannula. A thermistor (model 43TA, Yellow Springs Instruments) was inserted through the intercostal incision so that its tip lay among the abdominal viscera. Body temperature was maintained at 41°C by adjusting the temperature of the ventilating gas and the position of a heat lamp.

The bird was then positioned in sternal recumbency with the wings held in lateral extension (flying configuration) by attaching the four most distal primary flight feathers to vertical supports positioned distal to the manus (Fig. 1). Foam rubber was used to cushion the sternum and to assist in maintaining the bird in an upright position.

A sagittal incision was made over the dorsum of the left proximal brachium, and the tendon of insertion of M. triceps brachii was severed. The radial nerve was isolated where it crosses the dorsal surface of the humerus, freed from surrounding connective tissue, and severed as far proximally (deep to the triceps) as possible. The skin edge around the incision was sutured to a brass ring mounted in a micromanipulator (Fig. 1) to form a pool of mineral oil.
Single-unit recordings

Fiber bundles dissected from the radial nerve were placed across bipolar silver electrodes. Signals were amplified (model P511G with a high-impedance probe, Grass Instrument Co.), monitored with a storage oscilloscope (type 564, Tektronix) and audio monitor and recorded on an FM tape recorder (model 3960, Hewlett-Packard). Afferent nerve impulses, timing marks and spoken descriptions were recorded on the tape recorder at 15\text{inches s}^{-1} (38.1\text{cm s}^{-1})$, and the former were later replayed at 15/16\text{inches s}^{-1} (2.4\text{cm s}^{-1}) into the multichannel pen recorder for analysis.

Experimental protocol

After a nerve bundle had been placed across the electrodes, a probe was used to distort the skin gently and displace the feathers, in order to identify active afferent bundles in which there was no spontaneous activity, and to determine the general location of a receptor and whether it innervated a structure of interest. Single feathers were not manipulated during initial receptor identification, because of the time needed to find and

![Fig. 1. Experimental arrangement for measuring neural discharge during displacement of wing feathers; bird in ventral recumbancy. For details, see text. EC, electrode carrier positioned over the humeral shaft in mineral oil pool; AD, airflow delivery tube; CF, covert feather inserted into the propatagium being dorsally elevated with a probe; A, alula in cranial extension; SF, secondary feather; PF, primary feather; VS, vertical support of distal wing. Inset: relationship of filoplume feather (FP) and its follicle to the secondary flight feather and its follicle (SF); note that most of the filoplume is buried within the downy portion of the secondary feather.](image-url)
individually manipulate under magnification all the small coverts and filoplumes buried among the larger feathers, and because of damage to the feathers and feather surface produced by such a search. We focused our attention on discharge characteristics of the following mechanoreceptor–feather associations (Fig. 1): (1) alula receptors within the tissues supporting the alular joint (articulavis metacarpophalangealis alulae) between the carpometacarpus (major digit of manus) and digitus alulare (small cranial digit), (2) covert feather receptors on, or adjacent to, follicles of covert feathers (tectrices) on the dorsum of the wing and (3) secondary feather–filoplane receptors on filoplane follicles tightly adherent to the distal end of the follicles of secondary flight feathers (Fig. 1, inset).

When an airflow was used to perturb the feathers of the wing it was created using an air compressor (Craftsman 1.5 horsepower). The terminal 35cm segment of the delivery tube was made from 0.6cm i.d. polyvinylchloride tubing, with the discharge end of the delivery tube held 5–7cm cranial to the leading edge of the wing. Airflow velocity measurements were made using a hot-wire anemometer in the free stream over the dorsal antebrachium.

**Alula receptors**

The locations of the alular mechanoreceptors were established by probing the alular digit joint capsule. The alula was extended cranially (abducted) in the plane of the wing, to angles of 20, 40 or 60˚ in relation to the leading edge of the carpometacarpus, held in that position for 5s, and then returned to its initial position. Manual alular extension was produced using a metal probe. The angle of extension (±5˚) was determined from a template held along the leading edge of the carpometacarpus. The impulse discharge pattern of mechanoreceptors in the joint was continuously recorded during the movement. Three repetitions were completed at each angle. Movement velocity was not rigorously controlled or measured.

**Covert feather receptors**

The location of covert feather mechanoreceptors was established by deforming the skin with a probe. A receptor, located on or near the follicle of a covert feather, was stimulated by rapidly elevating the feather to an angle of 30, 60 or 90˚ from the plane of the wing (Fig. 1), maintaining it in that position for 5s, and then returning it to its initial position. Three repetitions were conducted at each angle. Movement velocity was not controlled or measured. Elevation of the covert deformed its rachis (quill) into a gently curved arc, so the angle of elevation (±5˚) was determined by the orientation of the distal half of the rachis with a template held atop the wing. The neural discharge was continuously recorded during each manipulation. Discharge frequency was also recorded with the feather held at 60˚ for 30s and with the feather moved up and down (30 repetitions) at 1s intervals (elevated for 1s, 0˚ for 1s). The position of the covert feathers was also altered, using an airstream (perpendicular to the span of the leading edge) directed across the wing at increasing angles of attack (0˚ to approximately 40˚ relative to the plane of the wing) to create airflow patterns (separation) that raised the covert feathers. The free-stream airflow velocity was approximately 4.2 ms⁻¹.
Secondary feather–filoplume receptors

To determine the location, adequate stimulus and discharge characteristics of a secondary feather–filoplume receptor, we (1) prodded the filoplume’s follicle, (2) manipulated the rachis of the filoplume, (3) moved the surrounding and overlying covert feathers, (4) vibrated the shaft of the secondary feather by dragging PE50 tubing along its barbs and (5) used an airflow of five different velocities (increased stepwise with a 15s interval between speed changes) directed at the leading edge of the wing (0° angle of attack). Neural discharge was continuously recorded as we increased the airflow velocity. The range of free-stream airflow velocities used was 0–14.6 ms\(^{-1}\). Velocity can be interpreted only from an ordinal perspective because, although we are confident of the maximum velocity (maximally opened valve), we simply used marked positions of the valve’s handle to produce the stepwise increase in airflow. Five different airflow velocities were used for each receptor; these were arbitrarily assigned the values of \(v_1\) for the lowest velocity to \(v_5\) for the highest velocity and are only roughly equivalent between receptors.

After the above manipulations, the filoplume shaft was severed where it emerged from the skin (Fig. 1, inset) and some of the tests were repeated. The rachis of the secondary feather was severed where it emerged from the skin (1 receptor) and the airflow manipulations were repeated with the filoplume associated with that feather present and intact.

Data analysis

Changes in discharge frequency associated with feather or joint movement were measured by counting impulses on the timed chart recordings. We determined both peak and static discharge frequency at each angle of extension of the alula and at each angle of elevation of the slowly adapting covert feather receptors. Peak discharge frequency was determined from the 4–6 impulses with the shortest interspike interval, and static discharge frequency was determined during a steady discharge for 1s. For the rapidly adapting covert feather receptors, only the peak discharge frequency was determined at each angle of feather elevation. Discharge frequencies were averaged over three repetitions at each angle. The average response for each type of receptor was determined by summing the discharge frequencies of all receptors, at each angle of elevation, and dividing by the number of receptors examined. Steady-state discharge frequencies of the secondary feather–filoplume receptors, in response to each stepwise increase in airflow velocity, were determined over a 10s period between the changes in airflow velocity. The discharge frequencies for 10 alternate 0.5s periods were averaged.

Results

Alula receptors

Probing of the alular joint established that these receptors were located within the supporting tissues of the joint and were not associated with the follicles of the alular feathers. Single-unit recordings were made from 10 slowly adapting mechanoreceptors...
(five birds), while the angle of extension (abduction) of the alula was extended to and maintained at 0, 20, 40 or 60°. Additional slowly adapting receptors were identified, but those were not analysed because they were not isolated as single units. We identified no rapidly adapting mechanoreceptors associated with the alular joint. Peak and static discharge frequencies increased in all receptors as the angle of extension of the alula increased (Fig. 2A), but there was variability between receptors (Fig. 2B). The average peak and static discharge frequencies of all 10 receptors, expressed as the percentage increase above the average static discharge frequency at 0° extension, are plotted in Fig. 2C.

**Covert feather receptors**

A variety of mechanoreceptors associated with the covert (contour) feathers of the dorsal wing were identified; we focused on receptors that were most responsive to dorsal feather elevation. We studied the discharge characteristics of 55 receptors (eight birds) associated with covert feathers arising from the propatagium. An additional 31 receptors were identified as belonging to this category but these could not be isolated as single units. The location of a receptor in relation to the follicles of the covert feathers was determined by direct probing of the skin. Action potential shapes were compared to ensure that the receptor responding to the probe was the same receptor that responded to feather movement. Some receptors were intimately associated with a covert feather’s
follicle, whereas others were located midway between follicles. Both of these arrangements formed a single class of mechanoreceptor–feather associations, subdivided into slowly adapting types (39 receptors) or rapidly adapting types (16 receptors).

The radial nerve innervated a large field of these receptors across the dorsal surface of the propatagium (i.e. the skin fold filling the space between the humerus and the antebrachium), extending distally from approximately 2cm proximal to the elbow as far as the proximal carpometacarpus. We did not find any mechanoreceptors innervated by the radial nerve associated with the curved covert feathers (tectrices marginales) inserted along the leading edge (cranial 1cm) of the propatagium. The major covert feathers located between the secondary flight feathers had slowly adapting mechanoreceptors associated with them, but their follicles were strongly attached to underlying tissues and the feather could not be elevated without simultaneously elevating the entire wing and/or damaging the feather’s rachis.

**Slowly adapting covert feather receptors**

Peak and static discharge frequencies of slowly adapting covert feather receptors increased when the angle of elevation of the covert feather was increased (Fig. 3A). The receptors’ sensitivity across the range of angles of feather elevation and their resting discharge frequencies varied between receptors (Fig. 3B,C). The average peak and static discharge frequencies, expressed as percentage increases above the average static discharge frequency at 0˚ elevation, are plotted in Fig. 3D.

These receptors did not show any significant adaptation (decreasing discharge frequency with time) when a feather was held in an elevated position for 30s. When a covert feather associated with a slowly adapting mechanoreceptor that discharged at rest (0˚) was returned to its resting position from an elevated position, the receptor ceased firing for 0–1.7s. The receptor discharge then returned to its resting (0˚) discharge frequency over the next 3.6s. Repeated feather elevations at 1s intervals caused no significant adaptation (change in discharge frequency during feather elevation) during 30 elevations of the feather. Each time the feather was returned to its resting position the discharge returned to a rate less than or equal to the resting discharge rate prior to the experimental manipulation.

An airstream directed at the leading edge of the wing produced dorsal displacement of the propatagial covert feathers when the angle of incidence of the airstream exceeded 10–15˚, and further increases in the angle of incidence produced higher feather elevation. Quantification of this angle of feather elevation was imprecise (in comparison to manual elevation), because many of the surrounding feathers were also dorsally displaced and because the feathers were in constant motion, moving through a vertical arc of approximately 5˚. Airflow angles of incidence above approximately 40˚ did not produce additional increases in feather elevation, but resulted in severe airflow turbulence which caused the feathers to vibrate and gyrate wildly. As the feathers were elevated by the airstream, the mechanoreceptors increased their discharge frequency (Fig. 4A). The static discharge frequency increased in a similar fashion during both manual and airflow elevation of the covert feathers (Fig. 4A). The obvious peak discharge period that immediately followed the elevation of a feather by hand was missing when the airstream
was used because of the slower graded elevation of the feathers (Fig. 4A). The static discharge was less regular during airflow elevation of the covert feathers than during manual elevation (Fig. 4A).

Rapidly adapting covert feather receptors

These receptors increased their discharge frequency and the number of impulses in their response as the angle of the covert feather was increased (Fig. 4B). They generated only a few impulses (4–16) when the feather was elevated and a few impulses when the feather was returned to its resting position. The peak discharge frequency and range of angular sensitivities in response to manual displacement varied between receptors (Fig. 5). This class of receptors was highly sensitive to specific angles of feather elevation.

Fig. 3. (A) Record of neural discharges from slowly adapting covert feather mechanoreceptors in response to different angles of covert feather elevation. Arrows indicate the time of feather elevation. (B,C) Responses of individual receptors to feather elevation; note the variability of different receptors’ responses to equivalent angles of feather elevation. Individual receptors are plotted on two graphs to highlight this variation. (D) Mean receptor sensitivity (%) (see Fig. 2) for peak and static responses plotted against angle of elevation for all slowly adapting covert feather receptors.
Although many of these receptors were initially stimulated when the feather was elevated to 30°, some were stimulated only at the highest angle of feather elevation (90°; Fig. 5). When the coverts were elevated by an airflow, the discharge of the rapidly adapting mechanoreceptors was similar to that seen with manual feather displacement: the receptors fired a burst of action potentials when the associated feather was elevated beyond its critical angle (e.g. 30° in Fig. 4B). Following the initial burst, these receptors continued to discharge at a much slower rate as the feather was further elevated by airflow applied at increasing angles of incidence (Fig. 4B). The increasing angle of feather elevation through which the receptor continued to discharge was variable between receptors, but in all cases was less than maximum feather elevation. Once the receptor had ceased to fire, it remained silent unless severe turbulence was created with an airflow angle of incidence greater than 40°.

Secondary feather–filoplume receptors

Rapidly adapting vibration-sensitive mechanoreceptors were associated with filoplume follicles that adhered tightly to the distal ends of the follicles of secondary flight feathers (Fig. 1 inset). Stimulating the skin with a narrow probe confirmed that these receptors were closely associated with filoplume follicles. These filoplume feathers were
completely covered by covert feathers, and the shaft and barbs of the filoplume were buried within the plumulaceous (downy) portion of the secondary feather (Fig. 1 inset). We have called these receptors ‘secondary feather–filoplume receptors’ because of their response characteristics (see below) and because the filoplume’s follicle was always tightly anchored to the follicle of the secondary feather. Vibration-sensitive mechanoreceptors innervated by the radial nerve were found in association with the follicles of small (less than 2cm in length) covert feathers or filoplumes covering the bird’s manus, but not in association with filoplumes attached to the follicles of the primary flight feathers. We did not find any primary feathers that responded in the fashion described below for the secondary feathers. Single-unit recordings were obtained from 13 secondary feather–filoplume receptors (six birds). We found no slowly adapting mechanoreceptors associated with filoplumes located on secondary feathers, but this may have been a result of the procedures that we used to identify the receptor initially, i.e. we did not attempt to manipulate each filoplume feather individually. Slowly adapting receptors were found along the follicles of primary and secondary feathers, but were not associated with filoplume follicles. These receptors were not sensitive to airflow over the wing, but discharged at less than 15Hz when the flight feathers were manually displaced and held in any direction.

Stimulating the filoplume follicle with a probe, or pulling on the filoplume, produced a burst of impulses which quickly ceased even though the stimulus remained constant. Only minute movements of the filoplume or a probe in contact with the filoplume’s follicle were required to induce another burst of action potentials. Movement of the covert feathers that surrounded and covered the filoplume did not elicit a response unless the dorsal wing surface formed by the covert feathers was significantly disrupted so that the covert feathers rubbed across the secondary feather associated with the filoplume’s follicle. Even then, only a small, inconsistent response (less than 5 impulses) was produced. Dragging the tip of a 10cm piece of PE50 tubing across the barbs of the vanes of the secondary feather associated with the filoplume follicle produced a repeatable
discharge whose frequency was related to the speed at which the tubing was moved (Fig. 6A). When the same stimulation was applied to secondary feathers adjacent to that under study, the response was greatly reduced or absent, i.e. vibration induced in one secondary feather is poorly transmitted to feathers with which it is in contact.

When an airflow was directed over the wing, the distal tips of the secondary feathers vibrated. The frequency of feather vibration appeared to be correlated with the stepwise increases in airflow velocity. Secondary feather–filoplume receptors responded to a steady airflow with a continuous discharge. As the airstream was moved medially or laterally away from the receptor, the discharge frequency was attenuated (Fig. 6B). When we held the airstream at the point that produced the maximum discharge frequency and increased the airflow from 0 to 14.6 m s$^{-1}$, the discharge frequency of the receptor increased (Fig. 7). At the highest airflow velocity, the recorded baselines of four receptors had rapid (frequency approximately equal to the discharge frequency), high-amplitude (greater than half the action potential amplitude) undulations that made accurate determination of the receptor discharge frequency impossible. All receptors continued to discharge at the highest airflow velocity, but the unreliable values were not included in Fig. 7.

Cutting off the filoplume where it emerged from the skin did not significantly alter the response of the receptor in its follicle to airflow over the secondary feather (Fig. 7C). However, cutting off the secondary feather (1 receptor), but leaving its associated filoplume present and intact, abolished the response of the receptor in the filoplume’s follicle to an airflow across the wing.

**Discussion**

Birds constantly adjust the size, shape, sweep, angle of incidence, dihedral and flapping amplitude and frequency of their wings in response to continuously changing flight conditions and demands. We suggest that the use of these adaptable wings for safe and efficient flight is dependent on a sensory system that detects two (or more) features of the

![Fig. 6. Neural discharges recorded from secondary feather–filoplume mechanoreceptors in response to (A) PE50 tubing being dragged across the barbs of secondary feather (fast versus slow) and (B) a constant airflow being moved from medial to lateral (5cm) along the leading edge of the wing.](image)
airflow over the wing: airspeed and separation of the airflow from the surface of the wing, which occurs during a stall. This study demonstrates that birds have mechanoreceptors associated with their wing feathers that might sense those two aerodynamic variables.

There are probably many different feather–mechanoreceptor associations on the bird’s body that respond in a meaningful way to airflow, and could thus be used during flight. Here we focus upon only three such associations found on the wing. The feathers and receptors identified here, together or in combination with other structures, may be capable of other sensory functions in addition to those discussed.

Fig. 7. (A) Recordings from two secondary feather–filoplume mechanoreceptors (1 and 2, not included in B) in response to five steps of increased airflow (v₁–v₅). (B) The discharge pattern of individual secondary feather–filoplume mechanoreceptors (each drawn as a different symbol) in response to steps of increased airflow. The bars represent the means of all secondary feather–filoplume mechanoreceptors. The position of the handle of the airflow control valve was used to regulate the increase in airflow, so that although v₅ (maximally opened valve) is the same for all receptors, v₁–v₄ are only roughly equivalent between receptors. All receptors continued to discharge at high frequency at the highest airflow velocity, but accurate interpretation of the discharge frequency was unreliable in four of the eight receptors because of large, high-frequency undulations of the baseline. (C) Responses of two secondary feather–filoplume receptors (different from those of A or B) to steps of increased airflow, with the filoplume intact (solid line) and after it had been removed (dashed line).
As the angle of incidence of a wing increases relative to the oncoming airflow, both lift and drag generated by the airfoil increase. There is a critical angle (15–20˚ in most aircraft) at which the drag increases dramatically, lift is essentially lost, and the wing is said to be stalled. At high angles of incidence, the airflow cannot smoothly follow the contour of the wing but instead begins to separate from the upper (dorsal) surface. Such separation begins at the trailing edge of the wing and advances towards the leading edge as the angle of incidence increases. Sensing the approach to the stalled condition (e.g. by sensing a high angle of incidence or airflow separation from the dorsal surface of the wing beginning at the trailing edge) might help birds avoid stalling (e.g. by reducing the angle of incidence or increasing thrust and/or lift production by flapping), or to exploit marginal flight conditions (e.g. hovering, slow flight or soaring).

Several muscles insert upon the alular digit and it appears capable of being actively moved, but extension of the alula during flight is thought to be a passive movement (Graham, 1930a,b,c; Brown, 1963; Nachtigall and Kempf, 1971) that occurs when the angle of incidence of the wing is increased during slow flight, landings and the downstroke of the wingbeat (Brown, 1963; Norberg, 1975; Pennycuick, 1975; Rüppell, 1980). When the wing exceeds a certain angle of incidence to the airflow, the alulae of deeply narcotized pigeons passively extend (D. Bilo, personal communication). We examined the range of alular extension angles seen in slow-motion cinematography of birds in flight (0–60˚, Rüppell, 1980).

High-speed cinematography and photography of birds in free flight show that the propatagial covert feathers are elevated by up to approximately 90˚ above the plane of the wing as a bird slows for landing and during certain portions of the wingbeat in slow and hovering flight (Rüppell, 1980). Nachtigall et al. (1985) demonstrated that the propatagial covert feathers on birds’ wings in a wind tunnel are dorsally elevated at angles of incidence greater than 10˚ by the airflow disturbances produced during flow separation.

We found a strong relationship between the angle of feather elevation or alular extension and the discharge frequency of mechanoreceptors located at the base of the covert feathers or within the tissues supporting the alular joint (Figs 2–5). The presence of both slowly and rapidly adapting receptors, their range of sensitivities and discharge outputs proportional to the angle of feather elevation provide a wide range of information to the central nervous system (Figs 3B,C, 5). Receptors distributed across the wing from shoulder to manus could provide information that would allow the bird’s central nervous system to detect how much of the wing surface is stalled (cranial advance of airflow separation point) and which section (medial to lateral) is stalled.

Using an airflow to elevate the coverts mimics what would occur in free flight, whereas the manual elevation of the coverts and alula to repeatable angles allowed us to compare the responses of receptors and to demonstrate a graded response to increasing displacement (i.e. feather elevation and alular extension). Variations of receptor response arising from the mechanical interactions of position, amplitude of displacement, velocity of displacement and direction of displacement (Skoglund, 1973; Burgess and Perl, 1973; Gottschaldt, 1985) render quantitative comparisons between manual and airflow...
displacement of the feathers unreliable. The robust results from these cited studies, which were designed to detect sensory mechanisms by which birds could sense the separation of the airflow from their wings, demonstrate that qualitative comparisons between airflow and manual feather displacement are valid. Furthermore, differences in the responses of receptors to the mechanical variables listed above could increase the overall specificity of information that these receptors are able to gather concerning flow separation (e.g., the rate at which the separation point advances towards the leading edge).

**Ability to assess speed of airflow over the wing**

Lift is proportional to the square of the velocity of the airflow over the wing. For any airfoil, there is an airspeed below which insufficient lift is produced to support the weight of the bird, and the wing will stall irrespective of the angle of incidence. Thus, airspeed information could be another indication of an imminent stall. Dynamic and thermal soaring, which are performed within a narrow range of optimal flying speeds, would be impractical without the ability to sense airspeed. The U-shaped curve that relates airspeed to the required aerodynamic power input predicts that, for all wings, there is a narrow range of ‘most efficient’ flight speeds that results in the lowest energy costs per unit distance traveled (Tucker, 1968; Pennycuick, 1968; Rayner, 1979a,b; Rothe and Nachtigall, 1985). Above and below this optimal airspeed, the cost of flight per unit distance covered is significantly increased. Thus, optimization of energy expenditure during flight (which is critically important for long over-water migrations) requires airspeed information. In addition, the most efficient wingbeat frequency and amplitude are closely correlated with airspeed (Rayner, 1981).

The distal ends of the secondary flight feathers can be seen to vibrate up and down rapidly in high-speed cinematography of flying birds (Rüppell, 1980). Our artificial airflow vibrated the secondary flight feathers at frequencies that were roughly correlated (by visual estimation) with the velocity of the airflow across the wing. During flight, all airfoils produce a continuous series of small vortices, named the von Kármán Vortex Street, that are shed alternately from the upper and lower surfaces of the trailing edge of the wing, and result in vibrations along that edge (Bénard, 1908a,b; Sherwood, 1946). The frequency with which vortices are formed and shed from an airfoil is directly related to the velocity of the airflow over that wing (Sherwood, 1946). We suggest that vibration in the secondary feathers would be an appropriate stimulus to be used as a quantitative indicator of airspeed.

We found a strong relationship between the airflow velocity over the wing and the discharge frequency of mechanoreceptors at the base of filoplumes located on the follicles of secondary flight feathers (Fig. 7). The range of airflow velocities we examined, 0–14.6 m s⁻¹, spans about half of the range of airspeeds within which most birds fly. The average of the reported maximum level flapping flight speeds for 131 taxa, measured under a variety of conditions, is approximately 14.7 m s⁻¹, with a range of 4.4–32.7 m s⁻¹ (Cooke, 1937; Pearson, 1961; Tucker and Schmidt-Koenig, 1971).

Although this class of mechanoreceptors was associated with the follicles of filoplumes (Fig. 1 inset), removal of the filoplume feather did not alter the mechanoreceptor’s response to graded airflow over the wing (Fig. 7C). Removal of the secondary flight
feather, however, eliminated all responses of the receptor to airflow over the wing, so we have designated these receptors as ‘secondary feather–filoplume receptors’. These receptors are quite sensitive and respond to vibrations of the secondary feather that appears to be smaller in amplitude than those produced by an airflow. Very low amplitude vibration of the secondary feather, produced by dragging thin, flexible plastic tubing (PE50) across the feather’s barbs, caused the mechanoreceptor to discharge at a frequency which was related to the rate at which the tubing was dragged (Fig. 6).

Airspeed over the wings fluctuates during the wingbeat cycle (Spedding, 1981). The instantaneous discharge frequencies of these receptors could provide the central nervous system with information about wing velocity, which is the critical factor in lift generation. Whole-body velocity information could be gained by averaging the airspeed velocity over the wings during the wingbeat cycle, by coordination between wingbeat kinematic receptors and the secondary feather–filoplume receptors, or by other sensors on the wing or body. The position of the secondary feather–filoplume receptors on the secondary feathers rather than on the more lateral primary feathers should reduce fluctuations in airspeed information during the wingbeat cycle.

Individual secondary feather–filoplume receptors were sensitive to airflow crossing only a small section of the wing (Fig. 6). During some flight maneuvers, the wing span is not perpendicular to the oncoming airflow. The bird’s body may then create an airflow shadow which deflects the airflow away from the proximal portion of one wing. The ability to sense differences in airflow velocity along the span of the wing may provide information about the orientation of the entire bird with reference to the oncoming airflow. The vibration-sensitive secondary feather–filoplume mechanoreceptors do not respond to wing vibration in general, at least with the stimulus used in these experiments, but are specific for vibrations of the secondary feathers themselves.

We show that the responses of the secondary feather–filoplume mechanoreceptors are largely unrelated to the presence of the filoplume feather. Although these results may not be applicable to all filoplumes and their receptors (e.g. slowly adapting filoplume mechanoreceptors associated with covert feathers; Necker, 1985a,b), they suggest that filoplume feathers may be evolutionary relics, i.e. degenerate feathers that are retained only for the mechanoreceptors associated with their follicles.

Most areas of the bird’s body are equipped with vibration-sensitive Herbst corpuscles (Hörster, 1990a,b; Gottschaldt, 1985). There are behavioral indications that breast and neck receptors may supply flight control information (Gewecke and Woike, 1978; Bilo and Bilo, 1983), but there is no evidence that they can detect airflow velocity. Airflow velocity can only be measured by mechanoreceptors if it is first converted into mechanical deformations of the receptor. Vibrations of the secondary feathers caused by the alternating vortices of the von Kármán Vortex Street may play such a role. Covert feathers were not commonly observed to vibrate in slow-motion films of birds in flight (Rüppell, 1980). Because of the strong relationship between airflow velocity and lift production (lift = velocity^2) and the role of the wings in lift production, sensory information regarding airflow velocity over the wings appears to be of primary concern for flight regulation.

Hörster (1990a,b) demonstrated a complex interaction between stimulus amplitude
and stimulus frequency on the discharge activity of vibration-sensitive, Herbst-like corpuscles within the skin of the manus, ECG and behavioral response of pigeons. Although the magnitude of the vortices of the von Kármán Vortex Street is increased with increasing angle of attack, the frequency of vortex shedding should remain relatively constant at incident angles below the stall. We are not aware of any quantitative reports of the frequency or magnitude of feather vibration during flight, or of the damping effect of the feather’s structure on vibrations. We are thus unable to evaluate the importance of Hörster’s (1990a,b) results. Flow separation (stall) creates chaotic airflow above the wing and laminar flow below the wing; this will affect feather vibration. However, we did not use such flow regimes to examine the secondary feather–filoplume receptors. Although the secondary feather–filoplume receptors supply information relevant to the stall (i.e. airspeed), we do not know whether they sense the airflow separation per se.

The use of a 0.6cm i.d. tube to produce an airflow across the wing does not duplicate the conditions encountered in free flight. However, we examined only feather movements similar to those that have been observed during free flight, so we consider that our results represent some of the ways in which a bird’s wing may detect airflow velocity during unrestrained flight.

In conclusion, birds have kinesthetic mechanoreceptors associated with their alular joint, which are activated by joint extension (abduction), and mechanoreceptors associated with the dorsal propatagial covert feathers, which are activated when the feathers are elevated. These receptors may supply information related to wing stalling. Mechanoreceptors in filoplume follicles associated with secondary flight feathers respond to vibrations of the secondary feathers with a discharge frequency that is correlated with the velocity of airflow over the wing. These receptors may supply information relevant to flying speed and to local airspeed over the wing.

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References


Airflow sensors in the avian wing


