

The biophysics of bird flight: functional relationships integrate aerodynamics, morphology, kinematics, muscles, and sensors¹

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Abstract: Bird flight is a remarkable adaptation that has allowed the approximately 10 000 extant species to colonize all terrestrial habitats on earth including high elevations, polar regions, distant islands, arid deserts, and many others. Birds exhibit numerous physiological and biomechanical adaptations for flight. Although bird flight is often studied at the level of aerodynamics, morphology, wingbeat kinematics, muscle activity, or sensory guidance independently, in reality these systems are naturally integrated. There has been an abundance of new studies in these mechanistic aspects of avian biology but comparatively less recent work on the physiological ecology of avian flight. Here we review research at the interface of the systems used in flight control and discuss several common themes. Modulation of aerodynamic forces to respond to different challenges is driven by three primary mechanisms: wing velocity about the shoulder, shape within the wing, and angle of attack. For birds that flap, the distinction between velocity and shape modulation synthesizes diverse studies in morphology, wing motion, and motor control. Recently developed tools for studying bird flight are influencing multiple areas of investigation, and in particular the role of sensory systems in flight control. How sensory information is transformed into motor commands in the avian brain remains, however, a largely unexplored frontier.

Key words: Aves, comparative biomechanics, neuromuscular control, visual guidance, wing morphing.

Résumé : Le vol des oiseaux est une adaptation remarquable qui a permis aux quelque 10 000 espèces actuelles de coloniser tous les habitats terrestres de la planète, dont les régions polaires et de haute altitude, les îles éloignées, les déserts arides et bien d'autres. Les oiseaux présentent de nombreuses adaptations physiologiques et biomécaniques pour le vol. Bien que l'aérodynamique, la morphologie, la cinématique des battements d'ailes, l'activité musculaire et le guidage sensoriel associés au vol d'oiseau soient souvent étudiés de manière indépendante, en réalité, ces systèmes sont naturellement intégrés. S'il y a abondance de nouvelles études sur ces aspects mécanistes de la biologie aviaire, moins de travaux récents se sont penchés sur l'écologie physiologique du vol des oiseaux. Nous passons en revue la recherche à l'interface des systèmes utilisés dans le contrôle du vol et abordons plusieurs thèmes communs. La modulation des forces aérodynamiques pour répondre à différents défis est assurée par trois principaux mécanismes, soit la vitesse des ailes autour de l'épaule, la forme à l'intérieur de l'aile et l'angle d'attaque. Pour les oiseaux qui battent des ailes, la distinction entre la modulation par la vitesse et par la forme regroupe des études variées sur la morphologie, le mouvement des ailes et le contrôle moteur. Des outils récemment mis au point pour étudier le vol des oiseaux influencent plusieurs champs d'étude, notamment le rôle des systèmes sensoriels dans le contrôle du vol. La transformation de l'information sensorielle en commandes motrices dans le cerveau des oiseaux demeure toutefois une frontière largement inexplorée. [Traduit par la Rédaction]

Mots-clés : oiseaux, biomécanique comparative, contrôle neuromusculaire, guidage visuel, morphing des ailes.

Introduction

The flying abilities of birds are impressive; casual observation of their soaring, hovering, and manoeuvring can lead one to assume that the graceful and poised motions are almost effortless. In reality, every one of the approximately 10 000 flying avian species is limited in its capacity to sense its environment and to generate and control aerodynamic forces. These sensory and biomechanical capabilities influence migration, foraging, mating, and competition—in essence, all of the ways that volant birds interact with their physical environment and with other organisms.

Flight evolved in the ancestor to modern birds during the Mesozoic period (Chiappe 2007) and has allowed this lineage to

diversify and occupy habitats throughout the world. Most of the extant avian lineages are highly capable fliers. Our understanding of early avian evolution has advanced considerably in recent years through the discovery of numerous Mesozoic fossils from the Jehol formation and elsewhere. The early evolution of flight has been a subject of ongoing research and debate since the discovery of *Archaeopteryx* Meyer, 1861 (Chatterjee 2015). Different schools of thought have incorporated biophysics into the evolutionary arguments, including aerodynamic theory (Burgers and Chiappe 1999), empirical measurements (Dial 2003), and experiments with robots (Peterson et al. 2011), models (Dyke et al. 2013), and across developmental stages (Dial et al. 2008). These studies illustrate the

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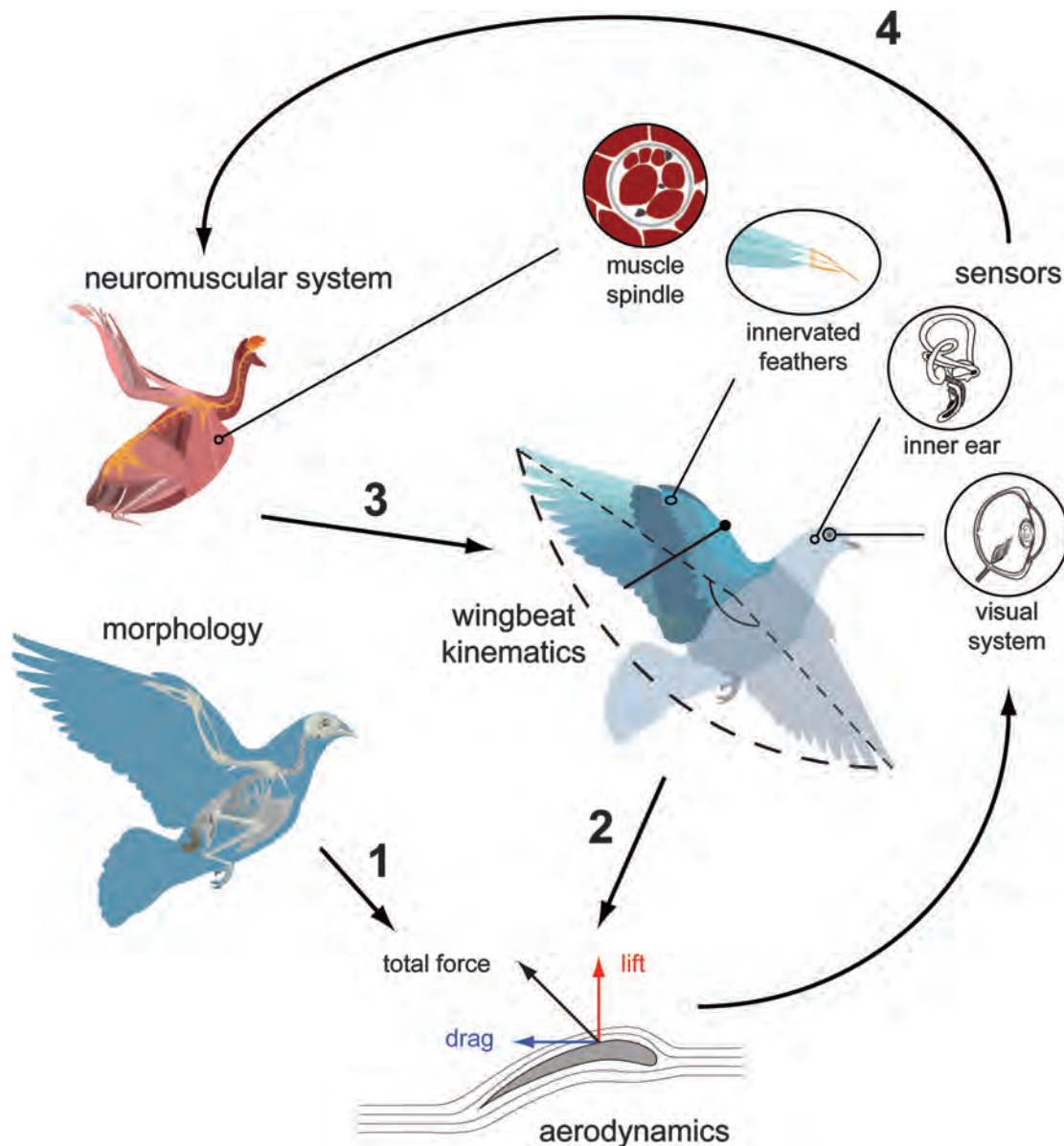
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Fig. 1. Integrated, multilevel systems approach to the study of bird flight. Aerodynamic forces are influenced by wing shape and wing motion. The latter is actively controlled by the neuromuscular system, which is informed by a diverse sensor suite. In this review, we describe research that integrates the function of these systems and emphasize the pathways that are best understood. Image of the pigeon created by and reproduced with permission of Phil Lai.



potential of using tools from biomechanics to study avian biology, in general, and evolution, in particular.

Researchers within the field of animal flight now often employ multilevel systems approaches (Fig. 1), which are borrowed from engineering, specifically controls and dynamical systems analysis and design. This framework facilitates examination of how multiple systems for controlling and powering flight are integrated to produce behaviour. The sensory system provides information from diverse sources to the nervous system, which then generates and organizes motor commands for the muscles. These act on the wings and body to produce aerodynamic force that lifts and propels, as well as drag for braking and torques for manoeuvring (Ros et al. 2015). Each level is initially modeled as a “black box” with intervening functional relationships that couple input and output parameters. Here we begin by outlining fundamental concepts of the aerodynamic forces powering bird flight. We then review the “upstream” connections by first examining how morphology (1)

and wing motion (2) influence aerodynamics, followed by how the muscles power and control the wings (3), and then how several key sensory systems inform the neuromuscular system (4). We conclude with a brief discussion of the prospects and challenges of integrating sensory physiology with motor output and of integrating mechanistic approaches with ecological and evolutionary research.

Aerodynamics

Bird wings are responsible for generating almost all of the aerodynamic forces required for flight, although the body and tail can also generate forces used for flight control and lift enhancement (Thomas 1996; Tobalske et al. 2009; Henningson et al. 2011; Henningson and Hedenström 2011; Muijres et al. 2012). This arrangement is in contrast to fixed-wing aircraft in which the functions of lift (i.e., weight support) and thrust are decoupled and

generated by the wings and either propellers or jets, respectively. The ability of birds to orient wing forces into both body weight support and thrust is possible because their wings move with respect to the body. This is facilitated by joints that provide degrees of freedom for wing motion around the shoulder (Hedrick et al. 2012) and for active shape change, i.e., morphing, with the arm and handwing (Lentink et al. 2007; Baier et al. 2013).

Aerodynamic force can be decomposed into separate components, and to quantify bird flight performance, we must consider lift, thrust, and drag in a body frame of reference. Lift is defined as the vector component perpendicular to the oncoming air, while thrust and drag are defined as vector components parallel to the oncoming air; thrust points in the direction of motion and drag points opposite. Because the forward body velocity orients the body reference frame in forward horizontal flight, lift supports weight and drag is opposed by thrust. To study the aerodynamic function of the wing, we must consider lift, thrust, and drag vectors in a wing frame of reference. A wing segment is considered in isolation and the force components are defined relative to the local velocity. Total wing velocity during flapping is composed of body velocity, which points forward, and relative wing motion, of which the magnitude and orientation depends on stroke angle, spanwise position, and angular velocity.

The wing downstroke is responsible for almost all weight support and thrust generation in the birds that have been studied to date (Tobalske 2007; Norberg 2011; Lentink et al. 2015; for a discussion see Crandell and Tobalske 2015), with the primary exception being hummingbirds (family Trochilidae) (Warrick et al. 2005). During the downstroke in forward flight, wing velocity points more downward and lift accordingly points more forward, thereby contributing to both weight support and thrust. However, the net function of the avian wing is more complicated. The inner part of the wing generates more drag than thrust, whereas the outer sections generate more thrust, which is sufficient to overcome the drag of the wing and body and propel the bird forward. How this works in detail has yet to be quantified in vivo.

To evaluate flight performance of the whole bird, the time-averaged equations for the force components are defined as:

$$(1) \quad \text{Lift} = C_L \frac{1}{2} \rho V^2 S$$

$$(2) \quad \text{Drag} = C_D \frac{1}{2} \rho V^2 S$$

$$(3) \quad \text{Thrust} = C_T \frac{1}{2} \rho V^2 S$$

Lift, drag, and thrust depend on properties of the wing such as surface area (S) that is actively controlled by the animal. Force components also depend on air density (ρ) that varies with altitude and incident velocity (V) at the location at which the pressure force effectively acts, the radius of gyration (Weis-Fogh 1973). Lift, drag, and thrust decrease with lower density and increase with greater wing surface area. The coefficients of lift (C_L), drag (C_D), and thrust (C_T) are dimensionless numbers that are primarily affected by the shape of the wing and the angle at which it encounters oncoming air, known as the angle of attack. These coefficients are calculated by measuring forces for a given angle of attack, density, wing surface area, and flight velocity typical for a particular species, after which the lift and drag equations can be solved for the coefficients. Because birds fly over a range of speeds that are relatively slow and because their wing-chord lengths (c) are small, the force coefficients depend strongly on the ratio of inertial versus viscous forces in the airflow (Shyy et al. 2013). Inertia force is proportional to density (ρ) and viscous forces are proportional to viscosity (μ) and the force ratio is estimated with the Reynolds number (Re):

$$(4) \quad Re = Vc \cdot \rho / \mu \approx Vc \cdot 68\,000$$

For birds flying near sea level, $\rho/\mu \approx 68\,000$ and Re ranges between about 5 000 and 15 000 for hummingbirds (Altshuler et al. 2004; Kruyt et al. 2014) to about a million for diving falcons (Swartz et al. 2008). Determining accurate aerodynamic force coefficients is well established for the high Reynolds number of fixed-wing aircraft, but more challenging for the low Reynolds numbers morphing wings of birds. Force coefficient calculations have been successfully applied in hovering (Usherwood 2009; Kruyt et al. 2014) and gliding (Withers 1981; Lentink et al. 2007) for prepared wings. Precise calculations based on in vivo measurements are considerably more difficult.

The aerodynamic equations illustrate how force can be modulated by altering wing shape (S , C_L , C_D , C_T) and airflow velocity (V) parameters. Based on the components of the aerodynamic force equations, we next distinguish between (1) kinematic variables that affect both wing area and force coefficients and (2) kinematic variables that affect wing velocity.

1. Wing shape and aerodynamics

The lifting surface of bird wings is composed of feathers that can be spread and folded to modulate force generation. Feather structural properties balance aerodynamic, ecological, and behavioural demands. Primary flight feathers are asymmetrically shaped with a stiff leading edge and long, flexible trailing edge, which helps the leading edge withstand the force of the oncoming air (Videler 2006). Owls have additionally evolved serrated leading-edge structures that contribute to silent flight (Bachmann and Wagner 2011). Differences in feather stiffness can be achieved through modifications to both material properties and structural architecture (Bachmann et al. 2012; Laurent et al. 2014). Flight feathers are susceptible to structural fatigue and breaking (Weber et al. 2005), and they are typically moulted and replaced annually (Weber et al. 2010), which can lead to seasonal differences in flight performance (Tucker 1991; Chai 1997).

Bird wings vary greatly in size and shape. Wing morphology is traditionally described in two dimensions, either the planform (top) or the profile (aerofoil, or cross section) view, following aeronautical conventions. In contrast to aircraft, however, both the planform and the profile are under musculoskeletal control in birds, yet they are mostly assumed constant to simplify aerodynamic analysis.

Wing planform is generally measured as wing area. Larger wings produce greater aerodynamic force (eqs. 1–3), but area changes in different regions of the wing can have varying impacts on performance (Videler 2006). In a manipulative study of House Sparrow (*Passer domesticus* L., 1758) wing area, it was demonstrated that cutting the tips of primary feathers dramatically reduced the distance flown, whereas removing all but the distal five primaries had no significant effect on flight distance (Brown and Cogley 1996). Flapping wings have lower velocity closer to the shoulder joint at low and moderate forward speeds because wing velocity is proportional to wing length (radius) multiplied by wing angular velocity. Removing distal wing area with higher local velocities will more strongly reduce aerodynamic force because force is proportional to velocity squared (eqs. 1–3). The relative span versus width of the wing is measured as aspect ratio, the wingspan over mean wing-chord length. The mean wing chord can be calculated as wingspan squared divided by surface area. The influence of aspect ratio on flight performance is strongly dependent on whether the wings are fixed or flapping and on the angle of attack (Kruyt et al. 2015).

Wing cross-section curvature of aircraft is usually measured as camber and affects the force coefficients, even for revolving model bird wings (Altshuler et al. 2004). However, static and dynamic camber are not well described for bird flight. Other mea-

tures of cross section include surface texture and roughness, which can also influence aerodynamic performance of bird wings (Klän et al. 2012; van Bokhorst et al. 2015). Additionally, birds have evolved a number of traits that are analogous to design features in fixed-wing aircraft. For example, the alula is a small projection on the front edge of the wing supported by the first digit, which is thought to function as a leading-edge slot (Nachtigall and Kempf 1971; Álvarez et al. 2001; Lee et al. 2015). Additionally, the covert and tail feathers can act as ailerons or flaps (Bechert et al. 2000; Lindhe Norberg 2002; Carruthers et al. 2007).

The diversity of bird wings is increased even further by changes in dynamic wing shape, known as wing morphing (Thomas 1996; Lindhe Norberg 2002; Lentink et al. 2007). Wing morphing can be both passive and active.

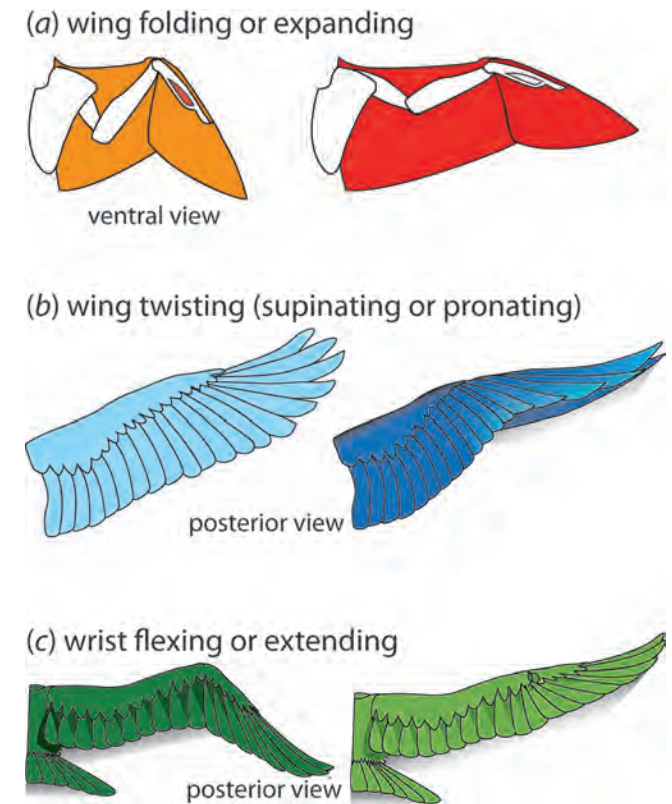
Passive wing morphing involves transient shape changes during flight that are not caused by muscle activity (Stowers and Lentink 2015). This should be strongly influenced by the structural and material properties of the wing anatomy and feathers. Tucker (Tucker 1993) measured slotted wings in a wind tunnel and found that bent feathers function as winglets to reduce drag. New methods with great potential for examining passive morphing in flight include marker tracking (Hedrick 2008; Song et al. 2014) and particle-correlation methods (Thomas et al. 2012; Martínez et al. 2015). Both techniques allow for measurement of three-dimensional surfaces and quantification of wing deformation through time.

Birds are further capable of active morphing within and across wingbeats because their wings have intrinsic muscles, skeletal joints, and spreadable feathers. The motion of intrinsic wing joints can be powered actively through muscles such as the biceps and triceps, or powered passively through inertial and aerodynamic forces during flapping while controlled by the muscles. Reconfigurable wing geometry greatly expands the range of possible flight behaviours by allowing birds to modulate aerodynamic force through changing the lift and drag coefficients, as well as wing area (Thomas 1996). Active morphing can modulate force production of static wings in soaring birds (e.g., Parrott 1970; Tucker and Parrott 1970), or modulate force within a flapping wingbeat, such as by reducing counterproductive upstroke forces. Much of this shape variation can be described with three kinematic variables: wing folding or expanding (Fig. 2a), wing twisting (Fig. 2b), and wrist flexing or extending (Fig. 2c).

In flapping flight, most birds fold the wing during the upstroke (Brown 1948, 1953, 1963), also known as the recovery stroke, by flexing the elbow and adducting the wrist (Robertson and Biewener 2012). Folding provides the dual benefit of shrinking the wing area to reduce counterproductive forces during the recovery stroke (Muijres et al. 2012) and shortening the span to lower the inertial cost of moving the wing (Riskin et al. 2012; Bahlman et al. 2013). Folding also varies with flight speed (Tobalske et al. 2003) and increases wing safety margins (decreases the risk of structural failure) at high speeds. An example of the latter case are Common Swift (*Apus apus* (L., 1758)) wings which can either be extended or swept, with swept wings less prone to structural failure (Lentink et al. 2007). Hummingbird wings fold less during hovering flight, but do exhibit some folding during the upstroke (Tanaka et al. 2013), and the degree of folding during both upstroke and downstroke changes with flight speed (Tobalske et al. 2007). Wing folding can also enhance flight control by allowing transient changes to maintain flight stability, such as tucking the wings in response to turbulence (Reynolds et al. 2014) or to navigate through clutter (Williams and Biewener 2015).

Wing twisting is defined as a change in the angle of incidence along the length of the wing (Fig. 2b). Whereas propellers are engineered to have static twist, the flapping wings of birds and other animals can dynamically twist, both passively and actively (Norberg 2011; Shyy et al. 2013). Passive twisting arises from mechanical forces given the structural and material properties of the wings. Active wing twisting is achieved through pronating and

supinating the wrist. Because wing velocity, and consequently angle of attack, naturally increase along the span of an untwisted wing, birds must twist their wings to normalize angle of attack and reduce stall at the wing tips. The angle of attack can vary considerably between the proximal wing and the distal wing (Hedrick et al. 2002). In extreme cases, birds can twist their wings until the wing tip is inverted, called tip reversal, which has been observed at slow speeds (Tobalske et al. 2003).



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Birds can bend their wings by flexing and extending the wrist dorsoventrally, i.e., perpendicular to the plane of the wing (Fig. 2c). Flexing the wrist allows the wing tip to travel a longer path, increasing wing-tip amplitude and wing-tip velocity, thereby enhancing aerodynamic force. Flexing the wrist during upstroke also reduces the wing's moment of inertia and redirects counterproductive upstroke forces from downward to lateral by reorienting the handwing more vertically. Wing folding and wrist flexing are often done simultaneously and have been referred to as wing flexing (i.e., Crandell and Tobalske 2015). The combination of wrist flexing and wing folding can also produce a cupped shape during the upstroke. Although we expect this configuration to be the least aerodynamically active, computational fluid dynamics models of similar cupped configurations in Peregrine Falcon (*Falco peregrinus* Tunstall, 1771) wings have demonstrated increased lift and decreased drag compared with uncupped configurations (Ponitz et al. 2014).

2. Wing motion and aerodynamics

Velocity has a major effect on lift production because aerodynamic force is proportional to velocity squared (eqs. 1–3). Total wing velocity is the vector sum of relative wing motion and body velocity. The strategies used by birds to increase total wing velocity may be highly dependent on physiological constraints and flight modes. Very large birds such as Andean Condors (*Vultur*

gryphus L., 1758) have large wings and limited ability to increase wing velocity by flapping (Pennycuick 1975), and therefore, increasing body velocity remains the most energetically efficient way to increase total wing velocity. Very small birds such as hummingbirds have very high wingbeat frequencies, and relative wing motion is the primary source of wing velocity. This likewise imposes limits on wing length, aerodynamic force production, and body size (Greenewalt 1962, 1975).

Relative wing motion can be altered by modulating wingbeat frequency, wingbeat amplitude, or the proportion of time spent in downstroke. Although amplitude and frequency affect aerodynamic force in similar ways, there is abundant evidence that hummingbirds prefer to increase amplitude over frequency. For example, when hummingbirds are challenged to fly at low air densities, they compensate by increasing wingbeat amplitude substantially, with relatively small changes in frequency (Chai and Dudley 1995, 1996; Altshuler and Dudley 2003). Hummingbirds also use a similar strategy of increasing amplitude more than frequency when challenged to fly with incrementally added weight (Mahalingam and Welch 2013). However, when the weight is increased to the point of maximal transient lifting performance, hummingbirds will increase both wingbeat frequency and amplitude (Chai et al. 1997; Altshuler and Dudley 2003; Altshuler et al. 2010a). The preference for increasing amplitude over frequency may reflect intrinsic properties of the flight muscles or the resonant frequency of the muscle–tendon complex that flaps the wing.

The aerodynamic consequences of wing motion have been studied with detached wings or wing models that are either fixed, revolving, or flapping. Fixed-wing preparations are useful for determining force coefficients of gliding birds (Withers 1981; Lentink et al. 2007). Flapping flight is substantially more complex with a gradient in velocity along the wing length and changes in acceleration and rotation within wing half-strokes. Velocity gradients can be studied by spinning wings or wing models about an axis instrumented with force sensors (Usherwood and Ellington 2002a, 2002b; Altshuler et al. 2004; Crandell and Tobalske 2011; Heers et al. 2011; Kruyt et al. 2014). Spinning wings effectively model the mid-downstroke of flapping wings, which is the period when velocity is greatest and aerodynamic forces are expected to be maximal. These preparations have demonstrated effects of variation in wing shape between half-strokes, across developmental stages, and among species (Usherwood and Ellington 2002b; Kruyt et al. 2014). The influence of changes in velocity and rotation on flapping aerodynamics has been examined using robotic flappers in the Reynolds number regime of insects (Ellington et al. 1996; Dickinson et al. 1999). These experiments have revealed aerodynamic effects that derive from wing wake interactions and are often concentrated at stroke reversal (Altshuler et al. 2005); similar effects may be present during flapping in birds (Hubel and Tropea 2010).

Wingbeat motion during steady-state flight modes has also been examined in flying birds. Studies in wind tunnels with variable speeds reveal different strategies for increasing force production to offset drag as speed increases. Hummingbirds increase wing-stroke amplitude only (Tobalske et al. 2007), whereas Budgerigars (*Melopsittacus undulatus* (Shaw, 1805)) and Zebra Finches (*Taeniopygia guttata* (Vieillot, 1817)) increase wingbeat frequency only at higher flight speeds (Ellerby and Askew 2007a), and still other birds like Black-billed Magpies (*Pica pica* (L., 1758)) increase both (Tobalske et al. 2003). Surprisingly, studies where pigeons were required to fly upward do not show changes in amplitude or frequency, suggesting that they use other mechanisms to increase force (Berg and Biewener 2008; Tobalske and Biewener 2008), such as angle of attack. Other birds may also use different strategies for modulating vertical and horizontal forces. Additional studies with load lifting would provide insight into the strategies used in this context.

Flying birds spend much of their airborne time stringing together sequences of manoeuvres. A manoeuvre is defined as any change in speed or direction; examples can range from simple changes (e.g., accelerations, decelerations, vertical climbs, descents, banked turns) to complex behaviours (e.g., crabbed turns, yaw turns, pitch–roll turns, skids, chandelle turns, barrel rolls). A common method for studying manoeuvrability is to provide birds with behavioural challenges that require them to perform a given manoeuvre in a repeatable way, such as taking off for horizontal (Warrick 1998) or vertical flight (Tobalske and Dial 2000; Berg and Biewener 2008; Jackson and Dial 2011), turning a corner in an L-shaped corridor (Hedrick and Biewener 2007; Hedrick et al. 2007; Ros et al. 2011), navigating an obstacle course (Warrick et al. 1988; Warrick and Dial 1998), or tracking a moving object (Altshuler et al. 2012). To perform all of these manoeuvres, flying animals increase aerodynamic force production beyond what is required for steady-state flight and then redirect the excess force to effect changes in momentum. Studies in which birds are required to accelerate have shown that they do so by increasing downstroke velocity through changes in wingbeat amplitude, frequency, and downstroke ratio. For linear accelerations, climbs, and banked turns, the wings are tilted forward, upwards, or laterally, respectively, often by reorienting the body. The magnitude of the aerodynamic force determines the amount of force available to be redirected while still supporting body weight. Body axis rotations may represent less costly methods of changing direction (Hedrick et al. 2009; Altshuler et al. 2012), although geometric and anatomical restrictions of wing shape, body shape, and shoulder excursion may limit the ability to roll, pitch, and yaw.

Changes in wing motion have profound effects on the wake structures produced by birds. As an airfoil moves through the air, it leaves behind a trail of vortices shed as a by-product of lift generation. Fixed-wing aircraft and gliders leave a relatively simple vortex wake: the vortices form a single elongated ring that starts at takeoff and ends at landing (Henningson and Hedenström 2011), provided angle of attack and airspeed do not change during cruise. In contrast, flapping animals leave complex vortex patterns that are influenced by wing shape and wingbeat kinematics. Animals that use aerodynamically inactive upstrokes leave a wake that resembles a series of discrete rings. Animals that supinate their wings to create aerodynamically active upstrokes leave a ladder-like vortex structure of connected rings (Kokshaysky 1979; Rayner 1979; Spedding et al. 1984; Spedding 1987). It has been proposed that some flying animals can transition between inactive upstrokes at low flight speeds and active upstrokes at high flight speeds, and this represents the aerial analog of discrete terrestrial gaits (Tobalske 2000; Hedrick et al. 2002). However, the transition may be more smooth and less discrete (Spedding et al. 2003). Some birds, such as hummingbirds (Warrick et al. 2005) and Common Swifts (Hubel et al. 2012), rely on active upstrokes.

3. Motor power and control

The motion of bird wings is controlled through the activity of bilaterally symmetrical muscle pairs. Just as we describe two functional categories of wing kinematics, we can make the same functional divisions of flight muscles. Kinematics that affect velocity, such as wingbeat frequency and amplitude, are controlled by two relatively large pectoral muscles that power the downstroke and upstroke, respectively: pectoralis major and supracoracoideus. Changes in force coefficients are achieved dynamically through changes in wing shape and orientation that are controlled by approximately 19 other smaller muscles crossing the shoulder and throughout the wing. The distribution and relative size of wing muscles differs among species (Dial et al. 1991; Dial 1992a; Welch and Altshuler 2009). Although we know a considerable amount about the large muscles powering the downstroke and

upstroke, the role of the intrinsic wing muscles in fine motor control is not well understood.

Downstroke velocity, and consequently force and power, are controlled primarily by the pectoralis major. This multipennate muscle is by far the largest muscle in flying birds, reflecting the importance of the downstroke in generating aerodynamic power for flight (Biewener 1998). Electromyographic recordings (EMG) from the pectoralis major reveal activation halfway through the upstroke, indicating that it not only plays a role in generating force to accelerate the wing downward, but also plays a role in slowing and reversing the upstroke (Dial et al. 1991). There is substantial evidence that the activation of the pectoralis major is actively tuned to match the aerodynamic power requirements of different flight behaviours. The myoelectric input measured using EMG can be analyzed as either the amplitudes of muscle potential spikes or as a rectified, integrated area of the EMG signal. The two measures often produce the same results and have been found to correlate with muscle force, strain, strain rate, work, and power for both hovering and forward flights. Examples come from Budgerigars (Ellerby and Askew 2007a, 2007b), Cockatiels (*Nymphicus hollandicus* (Kerr, 1792)) (Hedrick et al. 2003), Zebra Finches (Tobalske et al. 2005), hummingbirds (Anna's Hummingbird, *Calypte anna* (Lesson, 1829); Rufous Hummingbird, *Selasphorus rufus* (Gmelin, 1788)) (Altshuler et al. 2010b; Tobalske et al. 2010), Black-billed Magpies (Tobalske et al. 1997), pigeons (Tobalske and Biewener 2008), and European Starlings (*Sturnus vulgaris* L., 1758) (Tobalske 1995). Whereas EMG studies have provided considerable information about the timing and intensity of muscle contractions, direct measures of force and velocity are necessary to understand the mechanical power dynamics used to fly.

Arguably, the most important measurement for understanding muscle mechanical power is the work loop. A work loop derives from muscle force plotted against change in muscle length for a complete wingbeat cycle, the area of which represents the amount of work that has been done. Integrated over time, this measure is equivalent to mechanical power (Biewener et al. 1998). Both shape and area of the work loop are informative about control and performance and will vary with different flight modes. A key methodological advance in the study of flight muscle power was the development of a technique for *in vivo* force recording from the pectoralis major (Biewener et al. 1992). The pectoralis major broadly attaches to the keeled sternum and then narrows to an attachment area on the humerus. In some bird species (e.g., pigeons), there is a relatively flat extension just above the attachment point called the deltopectoral crest, which is a convenient place to attach a strain gauge. This technique has been applied multiple times on a variety of avian taxa in different experimental conditions including flight through corridors (Dial and Biewener 1993), wind tunnels (Dial et al. 1997), and ascending up vertical shafts (Jackson and Dial 2011).

The supracoracoideus muscle powers the upstroke. This muscle is attached broadly to the sternum, but its attachment to the humerus is more circuitous. The long supracoracoideus tendon passes through an opening in the coracoid bone and then loops over the top of the humerus. Muscle activity studies of the supracoracoideus indicate that this muscle is not only responsible for elevating the wing, but also supinating the wing, contributing to critical changes in angle of attack that reduce counterproductive upstroke forces (Tobalske and Biewener 2008). The upstroke can also generate aerodynamic lift in relatively large birds such as pigeons (Ros et al. 2011). However, the most significant aerodynamic contribution and largest relative size of supracoracoideus muscle is found in hummingbirds, where this muscle generates 25% or more of the required vertical force during hovering flight (Warrick et al. 2005).

The *in vivo* force recording technique originally developed for the pectoralis major has also been modified for recordings from supracoracoideus muscles (Tobalske and Biewener 2008). That

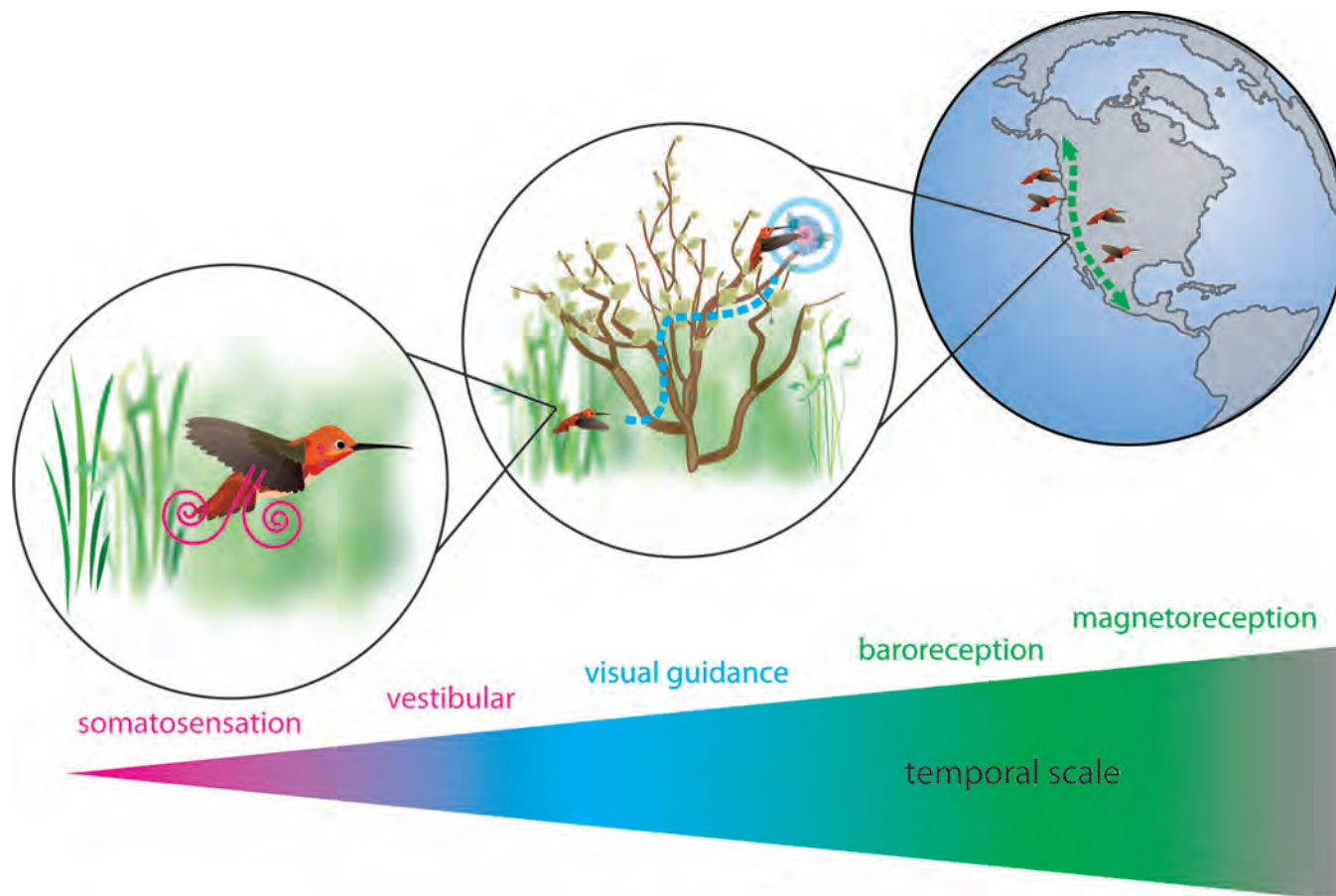
study revealed the duration of force generation is carefully controlled so that the antagonist pectoralis major and supracoracoideus muscles spend little time pulling against each other. The supracoracoideus also has an important role in elastic energy storage, as it reduces the required power output of the flight muscles. Clearly, the anatomy and physiology of this muscle represent some of the most important adaptations for avian flight.

Dynamic wing-shape changes are primarily controlled by a number of intrinsic wing muscles, whereas wing orientation is largely controlled by small shoulder muscles. The activation patterns of some of these shoulder and wing muscles were first characterized by Dial and co-workers for European Starlings flying over a range of speeds in a wind tunnel (Dial et al. 1991). This revealed that most of the recorded muscles were activated during stroke transitions. In an extraordinary follow up study, Dial (Dial 1992a) made recordings from 17 flight muscles in the pigeon, most of which were wing muscles, during four bilaterally symmetrical flight modes: takeoff, vertical ascent, level flapping, and landing. Again, most muscles were active during stroke transitions and there were only modest changes in timing for different flight modes. A similar study looking at muscle activity and muscle strain of the elbow flexors and extensors, as well as joint angles, revealed few differences in each of these measures between takeoff, landing, and steady flight (Robertson and Biewener 2012). However, EMG intensity revealed distinct patterns for different flight modes. The results suggest that flight modes that produce greater aerodynamic force, such as accelerating during takeoff, use higher intensity contractions of the intrinsic wing muscles. Thus, EMG intensity may be related to mechanical power requirements for different flight modes, even for the intrinsic wing muscles.

The role of the wing muscles in fine motor control has been more difficult to determine. Dial (Dial 1992b) made EMG recordings from flying pigeons after severing the nerves supplying the forearm muscles. Remarkably, the birds were able to sustain level flapping flight without active forearm muscles, but they were not able to take off without assistance or land correctly. There have been two studies of wing muscle activity patterns during turning flight. Hedrick and Biewener (Hedrick and Biewener 2007) recorded from the two pectoral muscles and two wing muscles of Rose-breasted Cockatoos (*Eolophus roseicapilla* (Vieillot, 1817)) as they turned in an L-shaped tunnel. They did not find any association between the measured muscle activation features and the changes in wingbeat kinematics or heading. Altshuler et al. (Altshuler et al. 2012) recorded from the pectoralis major and two wing muscles of Anna's Hummingbirds as they performed yaw turns while feeding from a revolving feeder. Again, they did not find any associations between muscle activation features and wingbeat kinematics or body position. Thus, although Dial's results implicate the intrinsic wing muscles for a role in fine motor control, there is not currently other support for this role.

Two potential limitations of previous studies of muscle activation during turns are that only a small fraction of the wing muscles were recorded and that the dynamic mechanical performance of these muscles is unknown. If the entire muscle system is orchestrated interactively, then the dynamic activity of one element might only become clear relative to the activity of other elements. It is known from other systems that changes in muscle activation can lead to a dramatic shifts in muscle roles, such as from a stiff to a compliant spring in the wing muscle of the blow fly *Calliphora vicina* Robineau-Desvoidy, 1830 (Tu and Dickinson 1994) or from a motor to a strut in the leg muscle of a running Wild Turkey (*Meleagris gallopavo* L., 1758) (Roberts et al. 1997). We suggest that moving forward in this area will require at least one of two challenging experimental approaches: recording from the full set of wing muscles during manoeuvres or combining *in vivo* measurements of wing muscle activity with *in vitro* measurements of work and power. Either approach should provide insight into

Fig. 3. Avian sensors inform flight control over different temporal and spatial scales. Somatosensory and vestibular feedbacks are relevant at the scale of wingbeats. Vision is used for stabilization and trajectory control and plays a role in long-distance navigation. Baroreception and magnetoreception provide information for landscape and global navigation.



whether there is segregation between power and control functions (Biewener 2011).

4. Sensory control of flight

Critical to controlling flight behaviour is a diverse suite of sensors that provide information for flight coordination and guidance. Various sensory systems provide information that is relevant on different temporal scales, therefore relating to behavioural control at different levels—from reflexes to route planning and navigation. At the finest temporal resolution is somatosensory feedback (Fig. 3), providing information about forces acting on the feathers and body. Body accelerations are sensed through the vestibular system (Fig. 3). Moving through an environment with visual features produces optic flow, a powerful visual signal for guiding and stabilizing a moving animal (Gibson 1950). Vision (Fig. 3) also provides information for navigation along with information contributed by sensors that provide baroreception and magnetoreception (Fig. 3) (O'Neill 2013). The information from these sensory systems is integrated to control flight. We briefly review how the sensors are specialized in avian taxa and describe what is known about the associated neural pathways that integrate and relay the information to motor centers. Although most studies of avian sensory systems discuss implications for flight performance, relatively few examine this link explicitly.

Somatosensory system

Mechanical forces acting on or within the body are detected by the somatosensory system. Mechanosensation can be extremely rapid, allowing fast responses to invisible stimuli, which may be

an advantage for the rapid manoeuvring often observed in bird flight. The low viscosity of air leads to pressure changes over a wider range of frequencies than in water and on land, which may have led to physiological specializations in avian somatosensation generally or even in specific groups of birds. Despite some classic behavioural experiments, the overall role of the mechanosensory system during flight has been difficult to study.

Mechanosensors aggregate around and ensheath feather follicles (Saxod 1996), indicating that birds may receive force feedback from all body feathers. How this translates to monitoring of forces is unknown, despite abundant anatomical and electrophysiological information about the receptors themselves (Necker 1983, 1985a; Gottschaldt 1985; Andres and von Düring 1990; Wild 1997, 2015). A reasonable hypothesis is that slowly adapting receptors like Merkel cells and Ruffini endings sense forces that lead to sustained feather and skin deformations, such as wind speed (Necker 1985b, 2000; Brown and Fedde 1993) and stall, whereas vibration receptors like Herbst corpuscles discriminate high-frequency elements of flow disturbances (Hörster 1990a). Herbst corpuscles are relatively well-studied elements of the avian somatosensory system and are rapidly adapting sensors that apparently fulfill the same function as the mammalian Pacinian corpuscle (Hörster 1990a). A very interesting difference lies in the best-response frequencies of each: whereas Pacinian corpuscles typically have best-response frequencies around 200–400 Hz, Herbst corpuscle best-response frequencies range from 100 to 900 Hz and can respond to stimuli even in the kilohertz range (Dorward 1970a; Hörster 1990a, 1990b).

Many of the major pathways to and among the avian central somatosensory nuclei are known (Wild 1997, 2015; Necker 2000). Representations of the body within nuclei have been examined and some exhibit ordered somatotopies (Wild 1997). Somatotopic organization varies greatly between major groups, with owls, Budgerigars, and pigeons all showing distinctly different organization in some nuclei (Wild 2015). However, despite abundant anatomical and physiological data from diverse species, it is unknown how somatosensory information is integrated in the avian brain. To this end, the cerebellum may be especially interesting. The cerebellar folia exhibit some somatotopy (Schulte and Necker 1998) and the evolution of “strong flight” in some lineages appears to have coincided with significant expansions in some folia (Iwaniuk et al. 2007).

The behavioural and neural responses of birds to somatosensory stimuli that would be received during flight are poorly described. In part, this is because movements of feathers in flight are poorly described. Brown and Fedde (Brown and Fedde 1993) demonstrated that neurons in the radial nerve respond proportionally to increases in airspeed over the wing, as well as to deflection of the coverts as may happen during stall. Similar high-frequency stimulation of the wing causes conditioned increase in heart rate (Shen 1983; Hörster 1990b), which is indirect evidence that wing afferent information affects behaviour. The most direct evidence of airflow sensing altering flight behaviour is that blowing on breast feathers causes birds to assume flight position (Bilo and Bilo 1978), whereas immobilising breast feathers subsequently restricts bounding flight (Gewecke and Woike 1978). It is unknown though whether the breast feathers convey detailed information about airflow, such as airspeed. The swirling air around the wings is presumably complicated to interpret and it remains unknown whether birds respond to signals from the wings. One anatomical indication that they do is that Herbst corpuscles appear to be particularly dense on the pigeon wing around the leading edge of the alula (Hörster 1990a), which should be an important site for detecting flow velocity.

In the absence of other evidence, we can only speculate on how mechanosensation is integrated into flight behaviour. Gliding birds that maintain shallow angles of attack may carefully monitor flow separation to prevent unintentional stall. Conversely, for birds that intentionally stall during landing, mechanosensation would help control the manoeuvre. If so, this might have contributed to Dial's (Dial 1992b) observation that Rock Doves (*Columba livia* Gmelin, 1789) were able to fly forward with a severed radialis nerve but unable to take off or land, which is a result of the loss of both efferent motor commands and afferent mechanosensory signals. The wings of insects and bats may be covered throughout in sensors, but most of the avian wing is flight feather. So although birds may be limited in their ability to sense backflow in a separation bubble or local deformations of the surface (Marshall et al. 2015), the long moment arm of flight feathers may afford an advantage for sensing low-frequency stimuli on the order of wingbeats.

A further advantage of the mechanosensory system over purely visual control is that bypassing processing in the brain would greatly reduce reaction times. Indeed, many aspects of flight stabilization may be solely reflex loops. For instance, pigeons that have undergone spinal transection produce sustained wing beating in response to muscle stretch (ten Cate 1936; ten Cate et al. 1937). Important insights have been gained from restrained birds, to which rotational moments can be applied and behaviours and muscle potentials recorded. This has demonstrated that visceral stretch receptors appear adequate for detecting and responding to body rotations, as behavioural compensation persists both after labyrinthectomy and spinal transection (Biederman-Thorson and Thorson 1973; Delius and Vollrath 1973). Compensatory tail flexing similarly persists after spinal transection (Bilo 1994). However, several aspects of the sensorimotor system are dependent on be-

havioural state (McArthur and Dickman 2011b), so the control of flight behaviour should be more complex than indicated by restrained birds.

In addition to deciphering changing flow conditions, birds must also monitor joint angles and length changes in muscles and tendons. Brown and Fedde (Brown and Fedde 1993) measured responses of slowly adapting receptors within the tissues of the alular joint, finding an approximately linear increase in discharge frequency with increasing alular extension. Muscle spindle and tendon organs monitor muscle and tendon movements, respectively. Bird muscle spindle morphology differs in some respects from those of mammals (Maier 1992), but muscle spindles and tendon organs of the two groups likely have similar physiological properties (Dorward 1970b).

Vestibular system

Birds have flexible necks and characteristically keep their heads fixed with respect to the horizon, regardless of changes in body axis orientation (Erichsen et al. 1989; Wohlschläger et al. 1993). When pigeons are launched into the air with their necks experimentally fixed, they are unable to stabilize the head and fall catastrophically out of the air (Warrick et al. 2002). This suggests that head stabilization reflexes are essential during flight (McArthur and Dickman 2011b). These reflexes are driven by visual and vestibular information (Gioanni 1988a, 1988b).

Vestibular reflexes can be isolated from visual input by testing birds in complete darkness. Compensatory eye and head motions triggered by the vestibular system are called vestibulo-ocular (VOR) and vestibulocollic (VCR) reflexes (Wilson et al. 1995; Gioanni and Sansonetti 1999; Haque and Dickman 2005). Vertical, horizontal, and torsional VOR have been measured in head-fixed pigeons during both translation and off-vertical axis rotations. The vertical and horizontal VOR motions in pigeons have gain functions similar to those of mammalian species, but pigeon rotational VOR gain values are lower (Gioanni 1988b; Dickman and Angelaki 1999; Dickman et al. 2000). Overall, the avian VOR undercompensates for perturbations in head-fixed conditions, but reflexive motions are able to completely compensate when VCR is allowed to contribute in head-free conditions (Haque and Dickman 2005), with similar results for visually induced reflexive eye and head motions (Gioanni 1988a).

In addition to stabilizing gaze, vestibular reflexes are important for posture control and stabilization of the relative positions of head and body during flight. Pigeons with breast feathers stimulated with air to simulate flight assume a gliding flight posture and exhibit wing- and tail-steering motions when the vestibular labyrinth is stimulated, unlike when they are in a resting posture (Bilo and Bilo 1978). This suggests that vestibular information contributes to tail control during pitch and roll motions in flying pigeons. Pitching or rolling pigeons in simulated flight conditions can also elicit body-stabilizing tail motion. In these conditions, the VOR and VCR exhibit increased gain, suggesting that a whole suite of compensatory reflexes are enhanced during flight (McArthur and Dickman 2011b). Neuronal activity underlying these compensatory reflexes was studied by recording from vestibular nuclear complex cells during rest and simulated flight. Three groups of motion-sensitive, state-dependent cells were identified. For two of these groups, spontaneous firing rates were increased during flight, whereas the third group responded to rotational motion only during simulated flight (McArthur and Dickman 2011a). How and where sensory information is integrated to produce these reflexive compensatory eye, head, and tail movements is not well described.

The cerebellum is a key site for integrating sensory information, including all of the vestibulo-mediated reflexes, and for coordinating motor commands. The cerebellum has what appears to be simple circuitry, but its function has proved difficult to define. It is a site of multimodal sensory and sensorimotor integration, as

well as complex, yet characteristic, neurochemical expression patterns (Voogd and Wylie 2004; Glickstein et al. 2009; Manto et al. 2012; Wylie et al. 2012; Aspden et al. 2015; Cerminara et al. 2015).

A subdivision of the avian cerebellum that has received considerable attention is the vestibulocerebellum (folia IXcd-X) (Winship and Wylie 2003, 2006). Optic flow input is integrated with vestibular information in the vestibulocerebellum, which is organized into parasagittal functional zones. The organization of zones that respond to rotational optic flow is thought to be highly conserved across mammals and birds (Voogd and Wylie 2004). For instance, Purkinje cells in the flocculus (lateral vestibulocerebellum) are involved in processing optic flow resulting from self-rotation, whereas the uvula-nodulus (medial vestibulocerebellum) processes optic flow resulting from self-translation. This aligns with retrograde tracing studies in pigeons showing that vestibular nuclei that project to the flocculus generally receive input from the semicircular canals, whereas regions of vestibular nuclei that project to the uvula-nodulus receive afferent projections from the otolith organs (Pakan et al. 2008). There is also a relationship between zebrin II (ZII) expression (parasagittal stripes) and the vestibulocerebellar optic flow zones in pigeons. Each ZII+/ZII-stripe pair aligns with an optic flow zone (horizontal axis rotation, vertical axis rotation, descent, contraction, expansion or ascent) (Pakan et al. 2011). Each optic flow zone contains neurons with the same rotational or translational motion preference, except for the ascent or expansion zone. Why this zone responds to two types of optic flow remains unknown.

The cerebellum could be a key site for determining and responding to state changes, as well as for regulating vestibular neurons responsible for initiating head, eye, and tail responses to motion. Shelhamer and Zee (Shelhamer and Zee 2003) have suggested that the cerebellum gates reflexes that generate vestibular head, eye, and limb movements according to behavioural state by switching between subpopulations of brain-stem neurons. Cerebellar neurons project to the vestibular nuclei of the brain stem (Arends and Zeigler 1991) and vestibulospinal neurons located in the lateral vestibular nucleus rhythmically increase spontaneous firing during locomotion (Orlovsky 1972; Marlinsky 1992). Behavioural and electrophysiological data suggest the presence of state-dependent gating of vestibular inputs to vestibulospinal neurons in pigeons (Rabin 1973, 1975). Therefore, functional zones in the cerebellum that receive multisensory inputs could respond to tightly regulated combinations of sensor activation to facilitate transitions between behavioural states in flight. Further investigation is required to identify whether state-dependent gating of vestibular projections to vestibulospinal neurons is the underlying pathway for state-dependent vestibular behaviours observed in birds and to better link molecular markers with function in the cerebellum.

Vision

Specialization of the avian eye and visual midbrain relative to other vertebrates suggests a key role for vision in flight control. Here, we first review research on the avian eye and behavioural studies of visual guidance. We next discuss the visual processing pathways in the avian brain, with special attention to motion processing.

Avian eyes have numerous specializations relative to the eyes of mammals. Most birds have large, laterally placed eyes with limited eye movement, which limits binocular overlap. With a few exceptions, notably owls, birds extract visual information from two largely nonoverlapping visual fields and rely on alternative processing mechanisms, such as motion parallax, to extract depth information (Martin 2007, 2009; Xiao and Frost 2013). The retinas of birds have four classes of single cones for processing colour information, as well as double cones involved in processing achromatic motion and luminance cues (Hunt et al. 2009). Birds are

also sensitive to light polarization (Muheim 2011), which is a key feature for navigation because it allows the use of polarized light at sunset and sunrise as calibration points for a sun-based compass.

The role for vision in controlling animal flight has been best described for the perception of visual motion. Optic flow is the movement of visual features across the eye and studies of insects indicate that perception of optic flow is critical for controlling several aspects of flight (Srinivasan et al. 1999; Taylor and Krapp 2007). More recently, there is evidence characterizing some optic-flow-based strategies for controlling flight speed and trajectory in birds. Budgerigars avoid vertically oriented gratings that produce high optic flow pattern velocities, flying towards horizontally oriented gratings and blank walls that produce no pattern velocity instead (Bhagavatula et al. 2011). Hummingbirds use visual motion to stabilize their position during hovering flight (Goller and Altshuler 2014). Flying Zebra Finches keep their heads steady during flight, isolating nonreflexive head motions to short bursts (Eckmeier et al. 2008), emphasizing the importance of stable vision for detecting and responding to self-motion.

Visual cues can also trigger stereotyped changes in flight behaviours, such as the wing-tucking behaviour of diving Northern Gannets (*Morus bassanus* (L., 1758)), wing positions for pigeons navigating clutter, and deceleration of hummingbirds docking with flowers (Lee and Reddish 1981; Lee et al. 1991; Williams and Biewener 2015). The flying animal's motion is not the only source of visual motion, however; the environment often contains other moving features such as other moving animals and wind-blown vegetation (Frost 2010). Behavioural studies of avian visual flight control have mainly focused on self-induced motion or optic flow, but perception of object motion is also important for many other behaviours during flight, such as foraging and predator avoidance. On relatively large birds, head-mounted cameras can be used to measure optic flow in situ (Kane and Zamani 2014; Kane et al. 2015). These methods have established that hunting Northern Goshawks (*Accipiter gentilis* (L., 1758)) often use a "constant absolute target direction" strategy to intercept moving prey initially, switching to direct "classical" pursuit depending on the context.

Given the influence of self-induced motion and object motion on flight behaviour, we next turn our attention to the neuronal populations underlying avian vision. There are three distinct neuronal pathways underlying vision in birds, which are homologous to the three primary mammalian pathways that carry visual information from the retina. In birds, these pathways are referred to as the accessory optic system (AOS), the thalamofugal pathway (retino-thalamic-Wulst), and the tectofugal pathway (tectoro-tundal-entopallial). Self-induced, global motion is generally processed in the AOS, whereas local motion generated by other moving objects or individuals is processed in the tectofugal pathway (Frost et al. 1990; Frost 2010). Here we briefly review components of the pretectum and AOS and tectofugal pathways with potential roles in motion processing during flight.

The two nuclei in the pretectum and AOS that receive retinal input are the nucleus lentiformis mesencephali (LM) and the nucleus of the basal optic root (nBOR). Self-motion is characterized by strong, directional visual motion, and AOS neurons in both the LM and nBOR have large receptive fields in the contralateral eye and respond to large-field stimuli moving in a preferred direction (Burns and Wallman 1981; Simpson 1984; Wylie and Crowder 2000; Crowder et al. 2003). The nuclei differ in the distributions of preferred directions with most nBOR neurons selective for the nasal-to-temporal direction, whereas the majority of LM cells are selective for the temporal-to-nasal direction. Other cells in the LM and nBOR respond to upward and downward motion as well.

In addition to directional selectivity, LM and nBOR neurons are also tuned in the spatiotemporal domain. Several studies have recorded the responses of LM and nBOR neurons to sine-wave

gratings while varying the temporal and spatial frequency, establishing that AOS neurons tuned to high temporal frequencies are also tuned to low spatial frequencies and vice versa (Wylie and Crowder 2000; Crowder and Wylie 2001; Crowder et al. 2003). This continuum from “fast” (high temporal and low spatial) to “slow” (low temporal and high spatial) cells may have functional significance for the use of self-motion cues over a range of flight modes. For instance, “slow” cells may be active in stabilization of hovering and slow flights, and “fast” cells in velocity control during cruising flight. As with direction preferences, the LM and nBOR play complementary roles in the pretectum and AOS pathway; the majority of LM neurons (2:1) are classed as fast cells, whereas the majority of nBOR neurons (3:1) are classed as slow cells. Interestingly, in hovering hummingbirds and to a lesser extent in transiently hovering species (especially kestrels (genus *Falco* L., 1758) and spinebills (genus *Acanthorhynchus* Gould, 1837)), it is the LM that is hypertrophied (Iwaniuk and Wylie 2007). This suggests that LM is specialized for hovering, but it is unknown how the distribution of fast and slow cells compares with flight-mode specializations among taxa.

The LM and nBOR neurons project to hindbrain areas important for the coordination of motor output to the flight muscles, including the medial column of the inferior olive and the vestibulocerebellum (Brauth and Karten 1977; Clarke 1977; Brecha et al. 1980; Lau et al. 1998). Although connections between motion-sensitive pretectal and AOS cells and pre-motor structures have been described, it is not yet known how the firing properties of these neurons influence flight control.

Another area with potential functional significance for flight is the nucleus rotundus (Rt), part of the tectofugal pathway that processes object motion. The ability to accurately measure image expansion is crucial for both interaction with objects and object avoidance during flight. Cell types that encode “time-to-collision” and rate of expansion parameters are located in the Rt (Sun and Frost 1998). The final locus in the tectofugal pathway, the entoptallium, also contains cells that respond to looming motion (Xiao et al. 2006), further supporting a key role for this pathway in object motion processing.

Despite the considerable work examining the neuroanatomy and cellular properties of nuclei in the tectofugal pathway and AOS, as well as the vestibulocerebellum (AOS input) and oculomotor cerebellum (tectofugal input) (Wylie 2013), the connections relaying information from these pathways through the cerebellum and on to downstream motor pathways remain undescribed. Although the neurons in each visual pathway respond differently to visual motion, it should be pointed out that visual motion simultaneously stimulates numerous pathways. Thus, a flying bird must integrate multiple streams of visual information and prioritize some pathways over others while moving through dynamic and complex environments.

Baroreception and magnetoreception

The ability to sense pressure and magnetic fields is important for altitude control and directional navigation in birds, especially for migratory species (Wiltschko and Wiltschko 1972; Mouritsen 2015). Baroreception is hypothesized to involve the paratympanic organ in the ear, but the evidence for the functional role of this structure is mixed (O’Neill 2013). In contrast, magnetoreception and its role in navigation is strongly supported by behavioural studies of migratory bird species exposed to different magnetic field treatments showing that birds can both detect and respond to changes in the strength and direction of magnetic fields (Mouritsen and Ritz 2005). There are at least three different avian structures that are able to transduce magnetic signals, described below, and all are located in proximity to other sensory organs.

A vision-derived magnetosensor is based on membrane-bound opsins in retinal photoreceptor cells that respond to magnetic fields. Sensitivity of these sensors is influenced by light wave-

length, intensity, and the amount of pre-exposure to light conditions. Some directionally selective cells in avian visual motion processing pathways also have preferred compass directions that increase firing rate (Wiltschko and Wiltschko 2002) and more recent work implicates the thalamofugal visual pathway as well (Ritz 2011; Wiltschko et al. 2011). Cluster N is a region of the forebrain that is necessary for magnetic compass orientation, but is not involved with visual navigation methods using the star compass or setting sun (Zapka et al. 2009; Mouritsen and Hore 2012).

Another magnetically sensitive structure is associated with the inner ear in the lagena (Wu and Dickman 2011), which may also be integrated with the baroreceptive paratympanic organ (O’Neill 2013). Lesioning the lagena suggested processing roles for the lateral hyperpallium, hippocampus, dorsal thalamus, and caudal vestibular nuclei, with a potential role of the vestibular brain stem as a magnetoreception integration site (Wu and Dickman 2012).

Lastly, magnetite structures found at the base of the upper bill in birds relay information about the intensity of magnetic fields, with evidence suggesting that this bill organ is not used for the magnetic compass (Wiltschko and Wiltschko 2013). Intensity information is sent through the ophthalmic branch of the trigeminal nerve to the principal trigeminal sensory nucleus and spinal trigeminal sensory nuclei, and though no direct connections to vestibular hindbrain nuclei are known, the potential for integration in the vestibular brain stem exists (Lefeldt et al. 2014).

Conclusions

This review covers diverse topics in avian morphology, wing motion, muscle activity, and sensory systems. We have sacrificed many of the details in each discipline to focus on research that explores the integration of these systems. The recent efforts to examine connections among flight control systems, especially with respect to motor output, stand in contrast to the relative lack of ecological and evolutionary integration, such as through comparative studies. We conclude with a brief discussion of the limits and potential for future work bridging studies of sensory physiology with motor control and for incorporating mechanistic approaches into studies of evolutionary ecology.

Research on the motor output of avian flight suggests that the influence of the force equations on aerodynamics extends upstream in flight control. Specifically, the force equations can be parsed into parameters that influence wing velocity and parameters that influence wing shape (wing area, force coefficients). There has been a rich history of work on wingbeat kinematics and their influence on force generation in diverse avian species. Although there have been many studies of how static wing shape influences aerodynamic forces, the dynamic changes in wing shape exhibited by birds represent an exciting direction for new research. The segregation between velocity and shape control is further reflected in the functional anatomy of the flight muscles. There is abundant evidence that the pectoral muscles are largely responsible for velocity control and a compelling hypothesis is that the intrinsic muscles of the wings are responsible for dynamic wing-shape change. An intriguing possibility is that the elements of the force equations are also represented in the organization of pre-motor nuclei in the brain, which to date remain largely undescribed.

Expanding our knowledge of pre-motor circuitry in birds is only the beginning of understanding flight control at the level of the central nervous system. We know little about how sensors are integrated and coordinated to control flight. To date it has proven difficult to apply even the “black box” approach to the central nervous system’s role in flight because defining which sensors provide important inputs and understanding the outputs to the muscles is nontrivial. As more efforts are made to characterize the sensory circuits and electrophysiology of flight muscle activation,

we slowly move closer to understanding the underlying control system.

Much of the progress described in this review has depended on the development of new technologies that enabled studies of bird flight in laboratories. Miniaturization of physiological and wireless sensors and development of diverse new technologies such as high-resolution, high-speed cameras and tracking systems continue to enable quantification of *in vivo* flight performance and underlying physiological processes. Looking ahead, behavioural tracking coupled with onboard cellular recording should allow for integration of sensory guidance with the properties of sensors, sensory brain areas, and the nuclei involved in sensorimotor integration. Virtual reality techniques and sophisticated closed-loop stimulus systems also are enabling experimentation where sensory systems can be manipulated during free-flight behaviour. Similarly, high-throughput techniques to quantify wing interactions with fluid media and measure muscle activity and wing properties during active flight should provide insight into the complex interaction between muscle activity, kinematics, and aerodynamic forces.

The majority of work that we have discussed in this review was conducted in the last 10–15 years, which has been a period of intensive investigation using improving technologies in the laboratory. We have learned a tremendous amount about diverse mechanisms in specific avian taxa, but we know relatively little about the generality of many findings across bird species or how these newly discovered mechanisms influence their ecology and evolution. Although ecological and evolutionary physiology were active research topics at the turn of last century, most of the recent advances in avian flight have concerned detailed mechanistic studies in the laboratory. It is our hope that the recent trajectory in research emphasis is reflective only of the restrictions of technology, which has necessitated the study of flight in highly controlled settings. We eagerly anticipate the further development of portable and robust tools (e.g., Theriault et al. 2014) for future work that focuses on broader ecological and evolutionary comparisons and measurements of how birds are behaving naturally in the field.

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