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Title

Pigeons produce aerodynamic torques through changes in wing trajectory during low speed aerial turns

Short Title

Aerodynamic torque generation in turning pigeons

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Pigeon; Turning; Aerodynamics; Dynamics Modeling; Inertia

Summary

The complexity of low speed maneuvering flight is apparent from the combination of two critical aspects of this behavior: high power and precise control. To understand how such control is achieved we examined the underlying kinematics and resulting aerodynamic mechanisms of low speed turning flight in the pigeon (*Columba livia*). Three birds were trained to perform 90-degree level turns in a stereotypical fashion and detailed three-dimensional (3D) kinematics were recorded at high speeds. Applying the angular momentum principle, we used mechanical modeling based on time-varying 3D inertia properties of individual sections of the pigeon's body to separate angular accelerations of the torso based on aerodynamics from those based on inertial effects. Directly measured angular accelerations of the torso were predicted by aerodynamic torques, justifying inferences of aerodynamic torque generation based on inside wing versus

outside wing kinematics. Surprisingly, contralateral asymmetries in wing speed did not appear to underlie the 90-degree aerial turns, nor did contralateral differences in wing area, angle of attack, wingbeat amplitude, or timing. Instead, torso angular accelerations into the turn were associated with the outside wing sweeping more anteriorly compared to a more laterally directed inside wing. In addition to moving through a relatively more retracted path, the inside wing was also more strongly pronated about its long axis compared with the outside wing, offsetting any difference in aerodynamic angle of attack that might arise from the observed asymmetry in wing trajectories. Therefore, to generate roll and pitch torques into the turn, pigeons simply reorient their wing trajectories toward the desired flight direction. As a result, by acting above the center of mass, the net aerodynamic force produced by the wings is directed inward, generating the necessary torques for turning.

Introduction

To gain insight into the control of flight maneuvers, an understanding of the mechanics and aerodynamics involved in turning is needed. However, to date turning flight has received little attention compared with steady forward flight.

Mechanistically, the task of turning consists of two conceptually separate components: 1) re-direction of the animal's flight path and 2) reorientation of the animal's body.

Re-direction of the flight path (involving changes in *translational movement*) requires centripetal force production. Slowly flying vertebrates, including horseshoe bats, pigeons, fruit bats and cockatoos, all bank to orient the net aerodynamic force into the turn, analogous to how fixed-wing aircraft turn (Aldridge, 1989; Warrick and Dial, 1998; Hedrick and Biewener, 2007; Iriarte-Diaz and Swartz, 2008; Ros *et al.*, 2011).

Reorientation of the torso (involving *rotational movement*) in flight can be achieved using two physical principles: (i) aerodynamic forces that induce torques about the center of mass (CM), and (ii) inertia-based changes in angular momentum of body segments that result in net changes in body orientation (Frolich, 1980; Hedrick *et al.*, 2007). 3D analysis of the mass distributions and time-varying configurations of the head, torso and wings can be used to determine both aerodynamics- and inertia-based maneuvering in flying birds.

Irrespective of the nature of the torque generating mechanisms, the initiation and active control of maneuvering flight requires asymmetries in force production by the animal's locomotor system. Thus, in order to identify underlying neuromuscular control mechanisms of turning flight, such mechanisms must be resolved on a fine timescale (within wingbeats). Prior work has shown that pigeons and cockatoos redirect net aerodynamic forces through bilateral asymmetries in both downstroke velocity and angular momentum of the two wings (Warrick and Dial, 1998; Hedrick *et al.* 2007). Furthermore, pigeons maneuvering through a course with multiple turns generate small, sequential, pectoralis muscle force asymmetries to bank and navigate through the course (Warrick *et al.* 1998).

Recently, we (Ros *et al.*, 2011) have shown that reorientations of the pigeon's torso are integral to low speed turning flight. Furthermore, torso rotations underlying flight path changes (constituting torque generation for steering) were found to occur subsequent to readily observable head rotations (head saccades) during the downstroke of the same wingbeat cycle (Ros and Biewener, in review). These torso rotations must be produced by torques resulting from asymmetrical force production by the wings and/or tail. Here we seek to identify the key mechanism underlying low speed turning in pigeons, by testing whether the relevant turning torques are of an aerodynamic or inertial nature, and by investigating how contralateral wing movement asymmetries underlie torque generation. Because wingbeats containing head saccades early in the turn likely display the strongest torque generation (Ros and Biewener, in review), eighteen specific wingbeats were selected for analysis (see Materials and Methods for details). Based on previous findings in pigeons, cockatoos and bats (Warrick and Dial, 1998; Hedrick *et al.* 2007; Iriarte-Diaz *et al.*, 2011), we expected inertial and aerodynamic effects to act synergistically in rotating the torso, because both aerodynamics-based and inertia-based torques would act in the opposite direction of a faster moving wing. We hypothesized further a greater influence of aerodynamic torques, generated through contralateral asymmetries in wing velocity and aerodynamic angle of attack (Warrick and Dial, 1998; Hedrick *et al.* 2007).

To test these hypotheses, we record detailed kinematics of three pigeons negotiating a level 90-degree turn (Fig. 1). By merging morphological mass-distribution measurements of the pigeon's wings, head, torso and tail with these positional data (Fig. 2), we generate a full three-dimensional (3D) dynamics model, which can separate aerodynamics-based from inertia-based angular accelerations of the turning pigeon's torso based on application of the conservation of angular momentum principle. A determination of the timing and magnitude of both aerodynamics- and inertia-based torso angular accelerations is expected to provide a more accurate description of the rotational component of the maneuver, as well as to allow for more a detailed identification of the wing and tail kinematics underlying these torso angular accelerations.

Results

The three pigeons negotiated the 90° level turns at a CM speed of $3.3 \pm 0.2 \text{ m s}^{-1}$ and a wingbeat frequency of $8.3 \pm 0.3 \text{ Hz}$. In terms of mass distribution, each wing (distal to the shoulder) comprised $6.3 \pm 0.7 \%$ and the head $3.9 \pm 0.3 \%$ of the bird's body mass ($319 \pm 33 \text{ g}$; Table 1).

Torso reorientations about all three anatomical axes

The low-speed, level turns were predominantly driven by roll and yaw rotations of the pigeons (Fig. 3). Only pitch fluctuated with consistent periodicity within the wingbeat cycle. Torso orientations about all three anatomical axes fluctuated within wingbeats, independent of changes in torso orientation across wingbeats. These latter net wingbeat reorientations about the roll and yaw torso axes, summed throughout the turn, comprised the majority of the torso reorientations across wingbeats (Table 2). The birds consistently yawed into the turn, whereas roll was initially directed into the turn and later directed outward from the turn. Net wingbeat pitch reorientations were generally directed upward (head-up).

Torque generation is based on aerodynamics

The angular momentum principle (Pratab and Ruina, 2009; Mitiguy, 2014) allowed for calculation of inertia-based angular accelerations of the torso, and, indirectly, for calculation of the aerodynamics-based equivalent. Using wing-segment masses and moments of inertia for the torso (which includes the tail) and head, the angular momentum principle was applied to the time-varying 3D marker positions. In brief, two separate main modeling steps were performed: (i) aerodynamics-based torques were estimated directly from the 3D positional data and morphological mass distributions; (ii) inertia-based torso angular acceleration were estimated based on the hypothetical case where the aerodynamic forces were assumed to be absent. The central angular momentum, *i.e.* the combined angular momentum of the entire body about the collective CM, can be calculated from time-varying mass distributions data (see Eqn 1). The aerodynamic torque follows directly from the rate change of the central angular momentum; whereas, by hypothetically equating the aerodynamic torque to zero the inertial angular effect of measured wing motions on the pigeon's torso can be inferred (see Materials and Methods section for details).

We found that aerodynamic torques, and not inertia-based angular momentum exchanges between the wings and the rest of the bird (torso, head and tail) predicted observed torso angular roll and pitch accelerations (Fig. 4). Estimated angular accelerations of the torso based on aerodynamics correlated positively with measured accelerations about each of the principal torso axes. These aerodynamics-based estimates most reliably predicted pitch rotations ($p < 0.01$, $R^2 = 0.89$), with significant torso acceleration correlations about both roll ($p < 0.01$, $R^2 = 0.72$) and yaw ($p < 0.01$, $R^2 = 0.62$) of similar strength. The range of estimated yaw accelerations was smallest, the only axis about which inertia-based estimates also predicted observed torso accelerations ($p < 0.01$, $R^2 = 0.41$; Fig 4). During the turning wingbeats selected for analysis of torque generating mechanisms, roll rotations were initiated early and arrested late in the downstroke, with a peak in angular velocity directed into the turn at mid downstroke (Fig. 5A & B). Variable roll velocities were of much smaller magnitude during the upstroke. Torso pitch velocities and accelerations consistently varied with wingbeat phase: head-up (positive) pitch acceleration peaked near the middle of upstroke and approximately two-thirds into downstroke, coincident with negative roll acceleration (out of the turn); whereas head-down (negative) pitch acceleration

146 peaked near the first third of downstroke, coincident with the peak in positive roll acceleration.
147 These pitch patterns were consistent for all wingbeats analyzed throughout the turn, and
148 consistent with aerodynamic torques (Fig. 8A & B). In contrast, torso roll and yaw aerodynamic
149 torques and resulting angular movements (not shown) were more variable throughout the turn.
150 Yaw velocity was consistently positive (directed into the turn) over the full wingbeat cycle (Fig.
151 5A), with a moderate deceleration phase near the end of downstroke (Fig. 5B).

153 *Model sensitivity and data validation*

154 Approaches containing double derivatives of positional data are sensitive to measuring errors,
155 warranting sensitivity tests of our dynamics model. Artificially varying the wing length by $\pm$
156 10% and changing the mass of the hand wings (the point masses distal to the wrist) by 10% of
157 the wing mass, did not change statistical trends between inertia- or aerodynamics-based and
158 observed angular torso accelerations. Artificially increasing the wing lengths or hand wing
159 masses resulted in a slightly reduced regression model fit between aerodynamics-based estimates
160 and observed torso angular accelerations (R^2 values for roll (0.72), pitch (0.89) and yaw (0.62)
161 decreased to 0.69, 0.87 and 0.56 for wing lengths, and decreased to or stayed equal at 0.64, 0.89
162 and 0.38 for hand wing masses, respectively). Artificially decreasing wing lengths or hand wing
163 masses lead to similar changes, but in the opposite direction. The sensitivity tests most strongly
164 affected torso acceleration estimates about the yaw axis, about which inertia-based estimates also
165 predicted observed torso angular accelerations, albeit with a lower slope (0.34 vs 0.66) and
166 regression model fit ($R^2=0.41$ vs 0.62) than aerodynamics-based estimates. Additionally, the
167 marker-based torso angular accelerations compared well to measurements obtained from a back-
168 mounted inertial measurement unit (IMU) in pigeons maneuvering at similar strengths and flight
169 speeds (Lin *et al.*, in prep). Besides similarities in trace shape within wingbeat cycles, peak torso
170 angular velocities and accelerations reached approximately 900 deg s^{-1} and $7 \cdot 10^4 \text{ deg s}^{-2}$,
171 respectively, for both kinematics derived and IMU-based values. Although the IMU recordings
172 were of pigeons during different maneuvers and should not be directly compared, their similar
173 patterns are affirmative and support the sensitivity tests in illustrating the robustness of our
174 finding of aerodynamics-based torque generation.

Torque generating mechanisms

Turning wingbeats selected for analysis of torque generating mechanisms were characterized by differentially swept wing trajectories, or paths of wing motion relative to the torso (Fig. 6), accompanied by contra-lateral differences in hand-wing axial (pronation-supination) orientation (Fig. 7A). Corresponding with the peak in roll acceleration observed early in downstroke (Fig 5B), the outside wing was initially positioned and swept more anteriorly compared to a more laterally directed inside wing trajectory (Fig 6). In concert with the contra-lateral asymmetry in wing trajectories, the inside wing was more strongly pronated, or rotated forward (leading-edge down) about the wing's long axis during the first half of the downstroke (Fig. 7A). This contra-lateral difference in pronation was reversed in the second half of the downstroke, through supination of the inside wing and pronation of the outside wing near the middle of the downstroke (Fig. 7A). As the pigeon's torso rolled into the turn in the downstroke (Fig. 5A), the inside wing also acquired a higher speed (Fig. 7B) and became oriented more laterally (Fig. 7C) compared with the outside wing.

Discussion

Aerodynamics- and inertia-based angular accelerations of pigeons' torsos during low speed turning flight were determined using segment masses, time-varying 3D inertia properties and torso and wing configurations. Using this approach, we show that measured torso angular accelerations correlate strongly with observed aerodynamic torques, justifying a comparison of inside wing versus outside wing kinematic proxies for aerodynamic torque generating mechanisms. In comparison to previous findings (Warrick and Dial, 1998), contralateral asymmetries in wing speed do not appear to underlie the aerial turns we analyzed, and surprisingly, nor do contralateral differences in wing area, angle of attack, wingbeat amplitude, or timing. Instead, to generate roll and pitch torques into the turn, the pigeons reorient their wing trajectories toward the desired direction while rotating their hand-wings such that similar aerodynamic angles of attack are maintained between the inside and outside wing (Figs. 6 & 7). As a result, the aerodynamic force is directed into the turn and, by acting above the center of mass, generates the necessary turning torques (Fig. 8).

Our results show that pigeons use a complex combination of roll, pitch and yaw torso rotations to make level turns, with the largest contribution resulting from reorientations about the antero-posterior axis of the torso (Fig. 2; Table 2). These roll rotations serve to redirect the net aerodynamic force, producing changes in the flight path (Ros *et al.*, 2011): during the first half of the turn pigeons roll into the turn, whereas during the second half they roll out. The observed roll patterns may also enable changes in torso pitch to contribute to the turn. Due to the bird's banked orientation while turning (Warrick and Dial, 1998; Hedrick and Biewener, 2007; Ros *et al.*, 2011), head-up pitch reorientations can contribute to reorienting the bird's body into the desired direction. However, neither the summed net wingbeat yaw or pitch reorientations fully matched the 90 degrees of the turn (Table 2), illustrating the need for a composite of whole-body rotation components to simultaneously meet the translational (flight path changes and gravitational support) and rotational (acquisition of the desired new flight orientation) requirements of the turn.

The consistent patterns of aerodynamics-based pitch acceleration and torque observed relative to wingbeat phase (Figs. 3, 5B, 8A & B), in combination with wing positioning throughout the wingbeat cycle, strongly suggest that the center of pressure of the resultant aerodynamic force is positioned dorsal to the bird's CM during the first half of downstroke, and ventral and anterior to the CM near the second half of downstroke, through the middle of upstroke. These inferences agree with previous findings that aerodynamic forces act dorsal to the center of mass during the downstroke of the Japanese White-eye (Su *et al.*, 2011) and corroborate the active aerodynamics of the pigeon's tip-reversal upstroke (Crandell and Tobalske, 2011; Ros *et al.*, 2011).

Contralateral differences in wing trajectory and hand-wing pronation (Figs. 6 & 7A) coincide with roll accelerations observed early in the downstroke that are directed towards the inside wing (Fig. 5B). Consequently, these kinematic asymmetries of the wings likely indicate the aerodynamic mechanism used to generate the necessary steering torque. Torso accelerations that increase the central angular momentum of the bird require differential activation of contralateral flight muscles. Compared to Warrick and Dial (1998), we find here that these 'active' torso angular accelerations do not correlate with contralateral asymmetries in wing speed relative to the torso (relevant from a control perspective), or in the inertial frame (relevant to

aerodynamics). Nor were contralateral differences in wing length (which may serve as a proxy for wing area), aerodynamic angle of attack, wingbeat amplitude, or timing found to correlate with observed patterns of torso angular acceleration. Instead, pigeons appear to reorient the flapping sweep of their wing trajectories toward the desired direction, while preventing aerodynamic angle of attack asymmetries through hand-wing rotations. These differences in wing trajectories between the inside and outside wing likely redirect the net aerodynamic force into the turn (Fig. 8D). Assuming that this aerodynamic force acts dorsal to the bird's CM, the redirected aerodynamic force would generate the observed roll towards the inside wing, in addition to producing head-down pitch (Fig. 8C & D).

Given broad similarities in the avian body plan and the fairly simple nature of the aerodynamic torque generating mechanism described here, we believe it is likely that other bird species use the same mechanism to generate aerodynamic torques during slow turning flight. For example, cockatoos turning at low speeds displayed contralateral differences in wing kinematics similar to those described here, even though these kinematic differences in the cockatoos did not relate significantly to roll accelerations (Hedrick and Biewener, 2007). It is likely that this reflects the greater kinematic resolution of the current study and recognition that redirection of aerodynamic force occurs at key points of turning that follow head saccades (Ros and Biewener, in review). Asymmetries in wing trajectory and pronation were also found previously in pigeons (Warrick and Dial, 1998). However, technical limitations prevented measurements of pronation angles throughout wingbeat cycles and, thus, linking these asymmetries to torque generation. In the current study, the eighteen turning wingbeats selected for analysis generally occurred early in the turn where the strongest trajectory changes occur (Ros *et al.*, 2011), although the described torque generating mechanism can be expected to be used throughout turns when trajectory changes are needed.

The observed contralateral differences in wing trajectory and hand-wing pronation further corroborate the idea that antebrachial musculature is involved in low speed flight maneuvers (Bilo, 1985; 1994; Dial, 1992). Our results, however, do not exclude the potential role of differential force production between contralateral pectoralis muscles of the inside and outside wing (Warrick *et al.*, 1998) or corresponding differential wing speeds (Warrick and Dial, 1998) as additional or complementary torque generating mechanisms. It is possible that our selection of

key turning wingbeats related to flight trajectory changes excluded other wingbeats in which wing speed asymmetries may contribute to torque production for turning. It is also likely that our improved resolution of temporal and spatial kinematics allow us improved accuracy for wing kinematics relative to movements of the bird's torso. Based on our analysis, we found that differences in wing speed occur near the middle and end of the downstroke (Fig. 7B), when roll velocities are substantial and are subsequently arrested (Fig. 5A). Because rotation of the torso increases the speed of the wing on the side of the bird that moves with torso roll (the inside wing), such a passive rotational damping mechanism (Hedrick *et al.*, 2009) may help to arrest the bird's roll velocity near the end of the downstroke. By projecting more laterally during the second half of downstroke (Figs. 6 & 7C), the inside wing's moment arm for aerodynamic force about the roll axis may also be increased, further enhancing rotational damping. To the extent that torso rotations are passively damped by these mechanisms, such torso rotations would mitigate the need for differential activation of contralateral wing muscles to arrest existing torso angular rotations.

Our mechanical modeling approach depends on second time-derivatives of estimated mass distributions, which renders it sensitive to the propagation of measuring errors. Therefore, we limit our conclusions based on the dynamics model to correlative patterns that indicate the nature of the torques underlying these turns (inertia or aerodynamics; Fig. 4) and to consistent aerodynamic pitch torques averaged over many turning wingbeats (Fig. 8A, B) that aid in interpreting the aerodynamic torque generating mechanism used to turn (Fig. 8C, D). More specific inferences, such as time-varying torque patterns within individual wingbeats, await further validation of the modeling and error analyses.

By examining the activation and strain patterns of flight muscles throughout aerial turns we plan to further explore the neuromuscular components of flight control. Differential activation of distal wing muscles has been found to relate to steering in simulated flight in pigeons (Bilo and Bilo, 1983). Additionally, the extensor metacarpus radialis, an antebrachial hand wing extensor, was found to predict lower frequency components of turning (Hedrick and Biewener, 2007). Differential activation of inside versus outside wing muscles that are likely to control wing trajectory, such as the scapulohumeralis caudalis and pectoralis pars sternobrachialis (Dial *et al.* 1991, Baier *et al.* 2013), and hand wing pronation, such as the

extensor metacarpi radialis and the ulnometacarpalis ventralis (Vasquez, 1995), may also play key roles in turning flight.

Materials and Methods

Animal training and flight recording

Three rock doves (*Columba livia*) were selected from 10 wild-caught individuals, based on their turning flight performance during training. These pigeons were housed, trained, and studied at the Concord Field Station (Bedford, MA) in accordance with protocols approved by Harvard University's Institutional Animal Care and Use Committee. The pigeons were trained to fly back and forth between two perches situated at either end of two 5-m-long by 1-m-wide by 2-m-high netted sections, connected by a 90° turn (Fig. 1). The symmetrical, square-corner corridor was constructed of lightweight, 2-cm mesh nylon deer netting supported by a PVC frame consisting of 4-cm diameter piping.

Flights were recorded simultaneously using two camera systems (see Ros *et al.*, 2011). A high-speed light video system recording at 250 Hz with 0.001 sec exposure time consisted of one FastCam-X 1280 PCI, two FastCam 1024 PCI cameras (Photron USA Inc., San Diego, CA, USA), and two RedLake PCI 500 cameras (RedLake Inc., San Diego, CA, USA). A second, infrared-based auto-tracking system recording at 240 Hz with 0.0004 sec exposure time consisted of six ProReflex MCU240 cameras (Qualisys AB, Göteborg, Sweden). The two camera systems were synchronized using an electrical pulse trigger.

Marker placement and 3D positional reconstruction

Using the eleven synchronized high-speed cameras, time-varying positions of 10 mm diameter torso and tail markers, as well as 4 mm diameter polystyrene wing markers were collected within a calibrated 1.8 m³ cubic volume that encompassed the turn. Trials accepted for analysis (> 90% of trials recorded) were those in which the birds (*i*) did not contact the netting and (*ii*) maintained a turning flight path relative to global horizontal of <5°. The markers were placed at 16 anatomical locations (see Ros *et al.*, 2011; Fig 2A): dorsum at the second thoracic vertebra; left and right rump (4-cm lateral to the vertebral column over the synsacrum); center of head; left and right wing roots; left and right wrists; tip of left and right fifth primary feathers;

67% of the length of left and right ninth primary feathers; 67% along the length of left and right outer tail feathers; left and right tip of the innermost secondary feathers. Elbow position was determined trigonometrically based on two lengths and three positions: brachial and antebrachial segment lengths and wing root, wrist, and tip of the innermost secondary feather positions. The maximum mass added to a bird by the markers, including elastic tape on the torso, was 14 g, or 4% of the body mass (BM).

The 3D marker positions were reconstructed based on the volumetric calibration, using freely available digitization software (Hedrick, 2008). Calculations were performed in Mathematica (Wolfram Research, Champaign, IL, USA) and Matlab (Mathworks Inc., Natick, MA, USA) using custom-written scripts. Positional data were filtered with a fourth-order Butterworth filter using a low-pass cutoff frequency three times the wingbeat frequency. Cutoff frequency was determined by residual analysis (Winter, 2005). To avoid poor performance of the Butterworth filter near the tails of time series (Walker, 1998), data from 15 frames on either end of each flight trial were omitted post-filtering. The aerodynamic torque filtered with the low-pass butterworth correlated strongly with a quintic spline ($R^2 = 0.98$).

Correlations between observed and estimated torso angular accelerations, based on one (peak) value per wingbeat, were tested with standard least squares regression models corrected for trial number, wingbeat number (relative to the geometrical center of the flight corridor, after Hedrick *et al.*, 2007) and individual effects (JMP, SAS Institute, Cary, NC). Unless noted otherwise, results were expressed as mean $\pm$ s.d.

Torso reorientations throughout the turn

Wingbeats were partitioned into upstroke and downstroke phases based on reversal of the major bending direction of the primary feathers. This reversal coincided with the instant the primary feather markers moved laterally relative to the torso, in both ventral (start of upstroke) and dorsal (start of downstroke) positions. Net wingbeat torso rotations were defined as the resulting changes in torso orientation over entire wingbeat periods and were calculated about each of the torso axes. For each of two left and two right turns per individual, at least five sequential upstroke-downstroke wingbeats were analyzed (22, 25 and 28 wingbeats for the three birds), over which net wingbeat torso rotations about each axis were accumulated over the course

of the 90° turn (Table 2). The analyzed spatial section of the flight corridor was kept consistent across individuals, with the measured change in flight path through the turn averaging to 90.0° ± 2.1° across individuals.

Dynamics modeling

The angular momentum principle states that the rate of change of the angular momentum of a system, *e.g.* an entire bird, about its center of mass is equal to the sum of all torques (used here to mean moments of force about the mass center) on the system (Mitiguy, 2014). For the body plan of a pigeon, with many spatial degrees of freedom, the central angular momentum can be calculated through summation of the angular momentum of each body segment about the collective, or system, center of mass (S_{CM}). S_{CM} can move relative to the torso, due primarily to varying wing and head positions.

To calculate the central angular momentum, a mass-distribution model was created that treated the torso/tail (modeled as one object) and head as rigid objects, and modeled each wing as a series of point masses P_i positioned along the wing segments (Fig. 2; Table 1). Here, the head was assumed to remain in a fixed orientation with respect to the torso and the mass of the tail was included in the torso, ignoring inertial effects due to independent head or tail movement relative to the torso. The wing segments were allocated based on wing anatomy (Fig. 2A). The moments of inertia about the antero-posterior (roll), medio-lateral (pitch), and dorso-ventral (yaw) axes of the head and torso (including the tail) (Table 3) were calculated from the angular swing periods during two-point suspensions (see Newman and Searle, 1957 and Alexander, 1968). Additionally, the centers of mass of the head and torso were determined by multiple single-point suspensions as the intersection of the direction of gravity. Only the wing markers were included in the morphometrics.

The angular momentum principle formulated with respect to S_{CM} states that angular momentum changes about the center of mass can only be achieved by external torques. Gravity produces a resultant force that acts through S_{CM} and thus does not apply a torque about S_{CM} . Aerodynamic forces are the only source of external torques about S_{CM} , and therefore the rate of change of the central angular momentum in the inertial reference frame N for the pigeon system

$S \left(\frac{{}^N d {}^N \vec{H}^{S/S_{CM}}}{dt} \right)$; Eqn 1) is equivalent to the aerodynamic torque acting about S_{CM} .

The expanded central angular momentum principle is given by (see Appendix for derivation):

$$\frac{{}^N d {}^N \vec{H}^{S/S_{CM}}}{dt} =$$

$$\left(\sum_{i=1}^n (m^{P_i} * [(\vec{r}^{P_i/T_{CM}} - A) (D + C + B)]) + (\underline{I}^{T/T_{CM}} \cdot {}^N \vec{\alpha}^T) + (m^T * D - A); \text{ (Eqn 1)} \right)$$

with:

$$A = \frac{1}{m^S} * \left(\sum_{i=1}^n (m^{P_i} * \vec{r}^{P_i/T_{CM}}) \right); \quad \text{(Eqn 2)}$$

$$B = {}^T \vec{a}^{P_i} + 2 {}^N \vec{\omega}^T \cdot {}^T \vec{v}^{P_i}; \quad \text{(Eqn 3)}$$

$$C = {}^N \vec{\alpha}^T \cdot \vec{r}^{P_i/T_{CM}} + {}^N \vec{\omega}^T \cdot ({}^N \vec{\omega}^T \cdot \vec{r}^{P_i/T_{CM}}); \quad \text{(Eqn 4)}$$

$$D = -\frac{1}{m^S} * \left(\sum_{i=1}^n (m^{P_i} * (B + C)) \right); \quad \text{(Eqn 5)}$$

for which

m^{P_i} = wing point mass P_i ;

m^S = mass of the system S (entire bird);

$\underline{I}^{T/T_{CM}}$ = inertia dyadic of the torso T about the center of mass of the torso;

$\vec{r}^{P_i/T_{CM}}$ = vector from the torso center of mass to P_i ;

${}^T \vec{v}^{P_i}$ = velocity of P_i in the reference frame of the torso;

${}^N \vec{\omega}^T$ = angular velocity of the torso in the inertial frame;

${}^T \vec{a}^{P_i}$ = acceleration of P_i in the reference frame of the torso;

${}^N \vec{\alpha}^T$ = angular acceleration of the torso in the inertial frame.

Even though the central angular momentum is only changed by external torques, relative movements of body segments result in redistributions of angular momentum, which can change the orientation of the pigeon in 3D space, much like a cat righting itself in mid-air (see Frolich, 1980). Specifically, in the absence of aerodynamic forces, the external torque about S_{CM} and, thus, the rate of change of the central angular momentum are zero. Therefore, any changes in the

angular momentum of the wings will be matched by an equal and opposite change in the angular momentum of the rest of the bird (torso, head and tail), referred to here as the torso-system. By equating the entire right-hand side of Eqn 1 to zero, the aerodynamic torque is assumed to be zero, and ${}^N\vec{\alpha}^{\text{Torso}}$ can be solved for at each time step (see Appendix). By comparing the *expected* angular velocity from inertia-based reorientations to the *measured* angular velocity of the torso, torso angular accelerations based on aerodynamic forces can, in turn, be deduced. Aerodynamics-based torso angular accelerations determined this way closely matched calculated aerodynamic torques in timing and direction (not shown) and were used for further analysis, as these torso angular accelerations could be directly compared with inertia-based torso angular accelerations.

Kinematics and aerodynamic torque generation

Potential wing kinematic predictors of aerodynamic torques were assessed on an inside wing vs outside wing basis. Accordingly, inside wing kinematics were averaged, as were outside wing kinematics, for wingbeat pairs obtained from left turn and right turns. Due to the incremental yet oscillatory nature of pigeon turning flight (Warrick *et al.*, 1998), wingbeat characteristics, such as variations in aerodynamic power output from one wingbeat to the next, could lead to higher wing speeds or angles of attack of both the inside and outside wings in a left turn as compared to a right turn (or *vice versa*), without accurately reflecting torque-related contralateral asymmetries. The averaging of inside wing versus outside wing kinematics for wingbeat pairs recorded across left and right turn flight trials accounted for such potential differences between wingbeat cycles, as well as differential left wing - right wing marker placement.

Even though active torque generation is required to change the orientation of a flying bird, once a bird has reoriented in a particular way, say banked into a turn, even subsequent wingbeats can change the flight direction, due to the previously obtained orientation. The challenge was to identify wingbeats with active torque generation that were of similar dynamic nature and of opposite sign, so that wingbeat pairs could be analyzed on the described inside versus outside wing basis.

Previously, we found that the occurrence of head saccades indicates wingbeats that contain active torque generation that lead to reorientations of the bird related to flight path changes (Ros and Biewener, in review). In addition to the before-mentioned wingbeat-to-wingbeat differences such as aerodynamic power and handedness, wingbeats can start with existing angular momentum, further complicating the identification of wingbeats to select for the analysis of torque generation. Eighteen key turning wingbeats (three left and three right per individual) were selected from wingbeats with large head saccades, generally occurring early in the turn, based on kinematic consistency in terms of torso angular velocity and acceleration profiles (Fig. 5). The selection of these key turning wingbeats was not based on wing kinematics. Consistent but opposing angular torso kinematics do not preclude differences in aerodynamic flight power or negate handedness, still requiring an inside versus outside wing analysis of the aerodynamic torque generating mechanism.

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Author Contributions

IGR and AAB designed and executed the research. IGR, MAB and ANP analyzed the data. All authors interpreted the results. IGR, AAB and LCB wrote the article.

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Figure Captions

Figure 1. Schematic top view of the flight corridor. Camera outlines represent viewing angles, with camera distances underrepresented by 50%, for the high-speed (blue) and infrared-based auto-tracking (red) systems. The spatially calibrated section of the 90-degree turn (dark blue), pigeon silhouettes, and perches (grey lines) are drawn to scale. Dimensions are noted along the outside of one leg of the symmetrical corridor.

Figure 2. Dynamics model of a pigeon based on marker locations. (A) Cut-out of a pigeon at mid downstroke, copper-coloured for contrast, with marker locations (black circles with white centers). The torso and head (hd) (large and small grey ellipsoids) were treated as rigid objects for which the moments of inertia were assigned about the principal torso axes (B): anterior-posterior (roll, red line), medio-lateral (pitch, green line) and dorso-ventral (yaw, blue line). The torso ellipsoid, which includes the tail, is positioned based the dorsal (dm) and rump (ru) markers. Per wing, three articulating segments (solid green lines) are represented by point masses: the brachium (one mass), antebrachium (two masses) and the hand wing distal to the wrist (eleven masses). Respectively, these segments are reconstructed based on the shoulder (sh) – elbow (el), elbow – wrist (wr) and wrist – center between the ninth (9p) and fifth (5p) primary markers. Each pointmass represents a wingstrip (in between the dashed green lines). The volumes of the spheres and ellipsoids represent relative masses. The dynamics model of a pigeon in late downstroke (B), and near mid-upstroke (C).

Figure 3. Low-speed, level turns in pigeons are predominantly based on roll and yaw rotations. Integrated angular velocities about the principal torso axes throughout a representative right turn, with positive roll and yaw into the turn, as well as head-up pitch (small depictions atop the figure). Initial angles are based on the inclinations of the corresponding torso axes with respect to the horizontal at the start of recording. The majority of torso reorientations occurs

about the roll and yaw axes. Only pitch varies periodically with the wingbeat (blue shading represents downstroke phases). Flight speed (grey trace), a one-wingbeat running average, remains approximately constant with a moderate slow down near the midpoint of the turn ($t = 0$ s).

Figure 4. Aerodynamic estimates predict torso angular accelerations. Torso angular accelerations based on aerodynamic torque estimates (“Aerodynamics”; left panels) predict measured torso accelerations throughout two left and two right turns per individual ($N=3$; plotted symbols), about roll (dark/red, top left; $R^2=0.72$, $p<0.01$), pitch (medium/green, center left; $R^2=0.89$, $p<0.01$) and yaw (light/blue, bottom left; $R^2=0.62$, $p<0.01$) axes. Torso angular accelerations based on rate of momentum exchange (“Inertia”; right panels) between the wings and the torso do not correlate with observed roll and pitch torso accelerations, but do correlate with observed yaw accelerations (light/blue, bottom right; $R^2=0.41$, $p<0.01$). The regression analyses about the principal torso axes are based on one (peak) torso acceleration per wingbeat and corrected for trial and wingbeat numbers and individual effects.

Figure 5. Roll velocity is initiated early and arrested late in the downstroke. (A) Mean $\pm$ sd of individual mean ($N=3$) torso velocities in roll (red), pitch (green) and yaw (blue) throughout three left and three right selected wingbeats early in the turn, and normalized to the wingbeat period. Near the middle of the downstroke (blue shading) the torso pitches bill-down (-) and rolls into the turn (+). (B) The mean individual roll and pitch accelerations peak in the first half of the downstroke (red and green, respectively), with extremes reversed in the second half of the downstroke, arresting the roll velocity and reversing the pitch velocities in (A), respectively. Pitch accelerations also show peaks near mid-upstroke, whereas roll accelerations are more variable during the upstroke.

Figure 6. Turning wingbeats are characterized by differentially swept wing trajectories. Mean $\pm$ sd (trace thickness) of individual mean trajectories of the distal wing marker for the inside (green) and outside (purple) wing for the same selected turning wingbeats as in Fig. 5. Both trajectories are represented as a right wing, by mirroring the left wing in the mid-sagittal plane. The trajectories are displayed relative to the torso frame, represented by the anterior (red),

right (green) and dorsal (blue) directions, as well as the right shoulder location (black sphere). The means of the 3D trajectories, with the upstroke in a lighter shade, are projected on each of the anatomical planes, emphasizing the more protracted (anteriorly projected) path of the outside wing early in the downstroke.

Figure 7. Wing pronation accompanies a more caudally swept inside wing, whereas a greater wing speed and later projection aerodynamically dampen roll velocity. (A) For the same wingbeats as in Fig. 5; 6, during the upstroke, the inside wing (green) and outside wing (purple) supinate and subsequently pronate about the wing long-axis in synchrony. Early in the downstroke, the inside wing pronates to a larger degree than the outside wing (purple), resulting in an inside versus outside wing differential that is negative, or pronated (black trace $\pm$ sd). The more pronated inside wing in combination with the contra-lateral difference in wing trajectory maintains comparable angles of attack between the wings. However, these wing-configuration and kinematic differences likely results in aerodynamic forces that act above the center of mass to be directed upwards and to the right side of the torso, causing the pitch down and roll torques into the turn. (B) Inside wing speed (of the ninth primary marker) starts surpassing outside wing speed as the roll velocity (A) increases towards the inside wing. The higher speed of the inside wing persists longer than the roll velocity, indicating its contribution to passive aerodynamic roll damping, aided by a more lateral orientation angle (C) of the inside wing (the angle between the wing long axis and the sagittal plane of the torso).

Figure 8. Interpretation of aerodynamic pitch and roll torques. Aerodynamic pitch torques, (A) normalized to the wingbeat cycle, of a representative individual (mean $\pm$ sd of 20 turning wingbeats) were (B) consistent across individuals (mean $\pm$ sd of individual means (N=3)). Negative (head-down) aerodynamic pitch torques early in downstroke and at the downstroke-upstroke transition are offset by positive peaks in pitch torque in the latter halves of both the upstroke and downstroke. These patterns, combined with wing stroke kinematics (Figs. 6 & 7), indicate that the resultant aerodynamic force acts behind S_{CM} (black-white symbol in C and D) during the early part of the downstroke and subsequently travels antero-ventrally to produce an opposing head-up torque by acting in front of S_{CM} later in downstroke. (C, D) Interpretation of

roll-in (C) and pitch-down (D) torque generating mechanisms. Rear-view of a cut-out of a pigeon entering a left turn, early in the downstroke, with superimposed anatomical roll (AP; red), pitch (ML; green) and yaw (DV; blue) axes (see Fig. 2B). (C) An approximation of the instantaneous 3D resultant aerodynamic force (black vector, F_{aero}) at this moment of the wingbeat cycle is projected onto the transverse ML-DV plane (teal dashed vector within the teal shading). The line of action (teal dotted line) of this transverse projection extends to the right of S_{CM} , with a moment arm (solid teal line) to produce a left roll torque into the turn (red circular arrow). A more pronated left wing and a more anteriorly swept right wing result in an aerodynamic force that is directed left of the mid-sagittal plane. (D) The 3D resultant aerodynamic force, F_{aero} , projected onto the mid-sagittal AP-DV plane (purple dashed vector within purple shading) acts, similarly, behind S_{CM} to produce a head-down pitch torque (green circular arrow). The picture was taken of a turning pigeon without markers.

Tables

Table 1. Morphological inertia properties measured for *Columba livia* (N=3): Segment masses.

Segment	% of BM
Torso (including tail)	83.6 ± 1.3
Head	3.9 ± 0.3
Brachium	1.5 ± 0.3
Ante-brachium	2.9 ± 0.4
Hand wing	1.9 ± 0.1

Table 2. Net wingbeat reorientations accumulated throughout the turn (N=3; individual means).

Torso rotation components	Reorientation (deg) (mean $\pm$ sd)
Roll	76.8 ± 13.6
Pitch	42.6 ± 1.6
Yaw	58.1 ± 4.3

Table 3. Morphological inertia properties measured for *Columba livia* (N=3): Mass moments of inertia (mean $\pm$ sd).

(*10 ⁻⁵ kg*m ²)	Roll	Pitch	Yaw
Torso	20.98 ± 3.75	56.38 ± 0.28	71.19 ± 8.62
Head	3.90 ± 0.45	5.93 ± 0.90	4.42 ± 0.13

A **B** **C**