Experimental Study of Low Speed Turning Flight in Cockatoos and Cockatiels

Tyson L. Hedrick
University of North Carolina, Chapel Hill, NC, 27599

Andrew A. Biewener
Harvard University, Cambridge, MA, 02138

An experimental study measuring the kinematics and neuromuscular activation patterns of turning flight in two bird species, cockatiels and rose-breasted cockatoos, was conducted to investigate the aerodynamic and neuromuscular asymmetries underlying avian maneuvering flight. Several individuals from both species were trained to perform turns while flying at low speed, ~3 m/s, through a netting corridor containing a 90 deg turn. During the turn the birds’ wing and body motions were measured with multi-camera high-speed videography. Analysis of these measurements showed that: 1) changes in heading occur exclusively in the downstroke phase of the wingbeat cycle, 2) changes in heading were accomplished by redirection of net aerodynamic force via body roll angles of up to 75 deg, 3) roll torque was generated during downstroke, and 4) the torque was the result of bilateral asymmetries in feathering angle and flapping amplitude. Despite large differences in body mass, ~300 g versus ~75 g, the cockatoos and cockatiels performed similarly with respect to turning rate and radius of turn. The cockatiels made more consistent use of flapping amplitude asymmetries.

Nomenclature

\begin{align*}
c &= \text{wing chord} \\
C_r &= \text{coefficient of resultant force} \\
f &= \text{flapping frequency} \\
I_x &= \text{moment of inertia about the X axis} \\
L_p &= \text{roll damping coefficient} \\
R &= \text{wing length} \\
\hat{r} &= \text{non-dimensional wing length} \\
v &= \text{wing velocity} \\
\beta &= \text{roll angle} \\
\dot{\beta} &= \text{roll velocity} \\
\ddot{\beta} &= \text{roll acceleration} \\
\theta &= \text{flapping amplitude} \\
\rho &= \text{air density} \\
\tau_l &= \text{torque due to the left wing} \\
\tau_r &= \text{torque due to the right wing} \\
\psi &= \text{heading} \\
\dot{\psi} &= \text{rate of change in heading}
\end{align*}

1 Assistant Professor, Department of Biology, CB# 3280 Coker Hall, AIAA Member
2 Lyman Professor of Biology, Department of Organismal and Evolutionary Biology

American Institute of Aeronautics and Astronautics
I. Introduction

Both biologists and engineers have long been fascinated by the remarkable aerial maneuverability of flying birds. However, few biologists have pursued experimental study of maneuvering in flapping fliers, a result of both the difficulty of collecting data from freely flying animals and the wealth of unanswered questions related to steady state flight performance. Furthermore, birds occupy a Reynolds number regime orders of magnitude below that of manned aircraft, reducing the applicability of lessons from avian flight to fixed wing, human scale flight. However, improvements in experimental methods for gathering data at improved spatial and temporal resolution, and growing interest in low Reynolds number UAVs have led to a number of recent experimental studies of avian maneuvering flight (e.g. Refs 1-5). Despite these efforts, a comprehensive and in-depth understanding of the aerodynamic and neuromuscular means used by birds to execute turns has not been reached. Here we describe the kinematics and muscle activation patterns of two species of birds, cockatiels and cockatoos, navigating a short flight course with a single, 90 degree turn.

II. Animals and Experimental Setup

We collected data from four captive cockatiels, *Nymphicus hollandicus*, and six rose-breasted cockatoos (hereafter cockatoos), *Eolophus roseicapillus*, (five wild-caught and one captive). The cockatiel experiments were conducted at Harvard University’s Concord Field Station in Massachusetts; whereas, the cockatoo experiments were performed at the University of Adelaide in South Australia. The birds were maintained as described in earlier reports4,6; all experiments were approved by the appropriate animal care and use committee.

Cockatiels and rose-breasted cockatoos are closely related species, both falling within the Australian parrot clade, the Cacatuidae7. Despite their close relationship, the two species differ substantially in body size but are similar in aspect ratio and wing loading (Table 1).

All birds were trained to fly between two perches positioned in an L-shaped flight corridor. The corridor was constructed of PVC pipe and orchard netting, confining the birds but permitting video cameras positioned outside the corridor to record the turns4. Three synchronized high speed video cameras (one Redlake PCI 500 and one Photron 1280X) were positioned about the periphery of the corridor with a shared image area centered on the 90 degree turn. This volume was calibrated via direct linear transformation8, permitting acquisition of three dimensional (3D) coordinate information from the birds as they flew through the corridor (Fig. 1).

Additionally, we collected electromyograms (EMGs) from the flight muscles of the birds via surgically implanted electrodes connected to a lightweight data cable. Implantation procedures and target muscles for the cockatoos are described in detail elsewhere4. Briefly, the birds were anesthetized to a surgical plane using isoflurane gas and the electrodes inserted in the muscles via incisions in the skin. The electrode leads were then passed under the skin to a common plug on the bird’s back. In the cockatoos we recorded from the left and right pectoralis, supracoracoideus, biceps and extensor metacarpi radialis muscles. The pectoralis muscle depresses the wing and is the main power and force generator. The supracoracoideus muscle elevates the wing, whereas the biceps and extensor metacarpi radialis are intrinsic to the wing and appear to influence wing shape and wing stroke amplitude1,9. Similar electrode implantation methods were used with the cockatiels, but owing to their smaller size we were only successful in placing implants in the left and right pectoralis muscles.

III. Experimental Results

Both bird species navigated the flight course at similar speeds and with similar overall flight kinematics (Table 2). All birds tended to maintain elevation while turning. Qualitatively, the cockatiels appeared to have little difficulty navigating the course, whereas the larger cockatoos appeared to struggle more. This likely reflected a combination of their greater flight speed but lower flapping frequency, requiring greater changes in heading during each wingbeat (Table 2). The greater difficulty experienced by the cockatoos was also reflected by their downstroke ratio being greater than one, typically reflective of birds flapping with high muscle power output10.
A. Roll and Change in Heading

In analyzing the kinematic data from each flight, we first computed the bird’s heading at each point in time from its instantaneous velocity vector in the horizontal plane. We then numbered the wingbeats in each series of flaps such that the 0th wingbeat was the first with a downstroke beginning after the bird completed 45 degrees of the 90 degree turn. Wingbeats were then characterized by both their flapping parameters such as amplitude, amplitude asymmetry and duration and by their average physical parameters, e.g. flight speed, roll angle, rate of change in heading. Analysis of these results clearly demonstrated that changes in heading were the result of roll into the turn (Fig. 2a). Furthermore, the vast majority of heading change occurred during the downstroke (Fig. 2b). These results support a simple and intuitive model that birds generate aerodynamic force primarily during downstroke and redirect that force into the turn via changes in body orientation. Thus, the question of how birds change direction becomes one of how birds change their body orientation during flight.

B. Changes in body orientation

Although the basic relationship between roll angle and rate of change in heading found in the turning birds is similar to the banked turns typical of fixed wing aircraft, the means by which birds change body angle differ from those of fixed wing aircraft. The instantaneous roll angle of a cockatiel engaged in a right-hand turn demonstrates some of the difficulties (Fig. 3a). Not only does roll change over the course of a turn, it also varies widely during each wingbeat cycle. These cyclic changes in body orientation are likely the result of the cockatiel flapping its wings through asymmetric arcs, as was demonstrated in an earlier analysis of cockatoo turn dynamics. Additionally, because birds have jointed wings that vary their moment of inertia throughout the stroke cycle, inertial effects may lead to net, as well as instantaneous, changes in body orientation. Therefore, the observed instantaneous changes in roll orientation are the result of both inertial and aerodynamic effects. Separating the two components by computing and removing the expected inertial changes in orientation would require higher resolution kinematics than were recorded in this study.

Table 2, Flapping parameters.

<table>
<thead>
<tr>
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<th>Cockatiels (n=4)</th>
<th>Cockatoos (n=6)</th>
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<tbody>
<tr>
<td>Flight speed, m/s</td>
<td>2.7 ± 0.4</td>
<td>3.1 ± 0.2</td>
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<tr>
<td>Wingbeat frequency, Hz</td>
<td>8.5 ± 0.9</td>
<td>7.8 ± 0.5</td>
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<tr>
<td>Wingbeat amplitude, deg</td>
<td>64.6 ± 11.2</td>
<td>73.7 ± 6.8</td>
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<tr>
<td>Downstroke:Upstroke ratio</td>
<td>0.88 ± 0.08</td>
<td>1.18 ± 0.11</td>
</tr>
<tr>
<td>Peak roll rate, deg/s</td>
<td>263.7 ± 25.8</td>
<td>350.3 ± 76.0</td>
</tr>
<tr>
<td>$I_x$, cm$^2$g</td>
<td>928 ± 111</td>
<td>12889 ± 937</td>
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All values are mean ± standard deviation. Roll rate was computed as the average for a complete wingbeat. The Downstroke : Upstroke ratio was computed from the duration of each phase of the stroke. The moment of inertia is for an extended-wing posture.
Additionally, the rapidly variation in roll angle within each stroke also complicates computation of useful roll velocities and roll accelerations. At any one instant, the derivatives will be dominated by the higher frequency signal, leading to derivatives that are not related to the overall change in body orientation. To address this, we fit a periodic function to the recorded roll angle time series by performing a simplex search about the 1st Fourier coefficient, minimizing the mean square error of the fit between the periodic function and the recorded angles (Fig 3a). We used the 1st and 2nd derivatives of the resulting periodic function in place of direct differentiation of the recorded data to obtain instantaneous roll velocity and acceleration characteristic of the whole-turn flight trajectory.

Finally, flapping fliers likely experience greater roll damping than fixed wing aircraft when engaged in low speed turns. Roll damping is enhanced because, at low flight speeds, the majority of airflow past the wings is due to the flapping motion itself, rather than the bird’s forward speed. Therefore, roll velocity creates meaningful asymmetries in wing velocity as well as angle of incidence in flapping fliers, as opposed to the unimportance of these velocity effects in fixed wing aircraft.

This effect can be demonstrated with a simple blade element analysis. Consider a two-dimensional cockatiel flapping its wings through a downstroke over an amplitude of 60 degrees at an overall wingbeat frequency of 8 Hz and moving at a forward speed of 3 m/s. The cockatiel’s roll damping relationship and characteristic coefficient, \( L_p \), may be stated as:

\[
d\hat{\beta} / dt = L_p \hat{\beta}
\]  

(1)

Assuming no external torque, Eq. (1) becomes the difference in roll torque provided by the two wings, divided by the bird’s moment of inertia, where the torques are a function of the roll velocity \( \hat{\beta} \).

\[
d\hat{\beta} / dt = (\tau_r - \tau_l) / I_x
\]

(2)

Recent experimental studies of flapping flight in birds suggests that, at slow flight speeds, bird wings experience high aerodynamic force coefficients similar to those found in insects, and that the aerodynamic forces are directed perpendicular to the wing. In this case, the torque about the X axis generated by the left wing is:

Figure 2 a), Roll angle versus rate of change in heading and b), rate of change in heading by wingbeat phase and number through the turn. The data in a) are an average wingbeat from each bird for each wingbeat number. The data in b) are an inter-individual mean and standard deviation for all cockatiel right turns. Wingbeat numbers are based on position in the turn, wingbeat 0 falls at mid-turn.
\[
\tau_i = (1/2) \rho R^2 \int_0^1 \dot{r} C_r c \left( \sqrt{(-\beta R \dot{r} + 2\theta R f)^2 + 3^2} \right)^2 \, d\dot{r}
\]  

For reasons of simplicity, Eq. (3) assumes that bird’s chord wing chord, \( c \), is constant and that the coefficient of resulting force, \( C_r \), typically a function of the wing’s angle of attack, is also constant. Finally, it assumes that the angular velocity of flapping is also constant. Our assumption of constant \( C_r \) will serve to reduce the final damping coefficient because increased force coefficients due to asymmetries in angle of incidence brought about by roll velocity are the primary source of roll damping in fixed wing aircraft.

As the only difference between Eq. (3) and a similar expression for the torque due to the right wing is the presence of the negative (rather than positive) \( \dot{\beta} \), Eq. (2) simplifies to:

\[
d\dot{\beta} / dt = -R^4 \rho c C_r \frac{\theta \dot{\beta}}{I_x}
\]  

Substituting the typical values of 0.3 for \( R \), 0.0325 for \( c \), 2.0 for \( C_r \) and the previously stated \( f \) of 8, \( \theta \) of \( \pi/3 \) radians and \( I_x \) from Table 2 into Eqn. (4) results in a roll damping constant, \( L_p \), of -57 s\(^{-1}\). This \( L_p \) gives a time constant less than a tenth of a wingbeat. Therefore, at least during downstroke we expect that, especially for the roll derivatives computed from the whole-turn periodic function, kinematic and neuromuscular patterns associated with roll will be manifest as correlations with roll velocity rather than roll acceleration.

In the cockatiels, we found that roll velocity was correlated with right – left asymmetry in the wing stroke amplitude in a body-fixed coordinate system (Fig 4a). The body-fixed coordinate rotates with the bird, so asymmetries in the wing stroke amplitude indicate asymmetry in the movement of the wings with respect to the shoulder joints, but not necessarily with respect to the surrounding fluid. However, wing stroke amplitude asymmetries in the world coordinate system were also present. These correlated strongly with roll acceleration over the course of the turn (Fig. 4b).

Despite the apparent similarity in turning mode and performance between the cockatoos and cockatiels, we did not find a similar set of correlations between wing stroke amplitude asymmetry in different coordinate systems and roll derivatives in the cockatoos. Wing stroke amplitude asymmetry in the global coordinate system was weakly, although significantly, correlated with roll acceleration, \((r^2 = 0.18, p < 0.05)\). However, there was no significant correlation between wing stroke amplitude asymmetry in the body coordinate system and roll velocity. Instead, cockatoos have been shown to use a combination of asymmetries in wing stroke amplitude, wing position with

Figure 3 a) Instantaneous roll orientation recorded from a cockatiel making a left turn, along with a periodic function at the whole turn frequency fit to the data. b) A power spectrum for the roll angle in a), demonstrating the existence of a strong secondary peak at wingbeat frequency, indicative of wing inertial effects on instantaneous roll orientation.

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C. Neuromuscular asymmetry during turning

Electromyograms recorded from the flight muscles of turning birds have the potential to reveal bilateral asymmetries in the activation input delivered to the flight motor muscles. As electromyogram intensity has been shown to relate linearly to muscle force and power in flying cockatiels\textsuperscript{10}, this potentially reveals asymmetries in force and torque at their source. However, analysis of the electromyograms recorded from the flight muscles of turning birds raised a number of difficulties. Firstly, the implants often failed due to mechanical stress imposed on the silver wire implants by the bird’s motion. Due to these difficulties, we were only able to record electromyograms from two of the four cockatiels. As described elsewhere\textsuperscript{5}, we had greater success with the larger cockatoos, but still encountered an implant failure rate of approximately 33%. Secondly, the motion of the data cable and of the electromyogram wires under the bird’s skin adds low frequency noise to the recorded signals. However, these disturbances occur at a low signal frequency (< 60 Hz) when compared to the actual electromyograms of flying birds (500 – 1000 Hz) and were removed by application of a 60 – 1500 Hz zero lag bandpass filter (4 pole digital Butterworth). Finally, differences in electrode geometry and placement within a muscle lead to differences in the signal recorded from each implant\textsuperscript{15}. To standardize the EMG data recorded from each muscle we first rectified the signal, and then measured the mean voltage of each discrete muscle activation event, i.e. of each wingbeat. Once we had collected mean values from all bursts in an individual muscle, encompassing both left and right turns, we divided the value of each burst by the standard deviation of the population of bursts and then subtracted the population mean. This resulted in a group of standardized burst values with a mean of zero and a variance of one, removing the effects of inter-electrode variation. Finally, we measured burst asymmetry by subtracting the left burst from the right burst for each wingbeat.

We found prominent bilateral asymmetries in the neuromuscular activation of the pectoralis muscle in each of the two cockatiels. As shown in Fig 5a, the outside wing pectoralis received greater activation in the early portion of the turn. The trend reversed after the middle of the turn, when the inside wing pectoralis received greater activation. The resulting pattern of activation asymmetry matches the roll velocity derived from the periodic function fit to the overall pattern of body roll, both in the general pattern and statistically when the activation asymmetries common to discrete wingbeats were matched to the measured roll accelerations (Fig. 5b). Pectoralis activation asymmetry was also weakly correlated with the body coordinate system wing stroke amplitude asymmetries, $r^2 = 0.18$, $p < 0.05$ (two sided t-test of the slope, the intercept was not significantly different from 0).

Figure 4 a), The relationship between body coordinate system downstroke amplitude asymmetry and roll velocity. b), The relationship between downstroke amplitude asymmetry in the world coordinate system and roll acceleration and Data are from the cockatiels and represent an average wingbeat from each bird for each wingbeat number. Positive roll is to the right and a positive arc asymmetry indicates a larger arc on the right wing.
As with the wing kinematic correlates to changes in body orientation, the cockatiel results were not replicated in the cockatoos. In the cockatoos, pectoralis muscle activation asymmetries were smaller and asymmetries in some of the other flight muscles also contributed significantly to different kinematic asymmetries related to turning.

IV. Conclusion

We found that both cockatoos and cockatiels executed low speed, 90 degree turns by establishing bank angles of up to 60 degrees while flapping through the turn. Rate of change in heading was linearly related to bank angle, and rate of change in heading was much greater during the downstroke phase of each wingbeat cycle. The smaller cockatiels appeared to have less difficulty performing the turn than their larger cousins, but all individuals in the study were able to successfully complete the flight course. Because changes in heading were strongly dependent on roll orientation, the remainder of our analysis focused on aerodynamic and neuromuscular means that the birds might use to change body orientation. However, examination of the instantaneous roll orientation records revealed that roll orientation changes dramatically within each wingbeat cycle, likely in response to the inertial effects of the bird flapping its wings through asymmetric arcs. Furthermore, because the moment of inertia of bird wings changes throughout the stroke, these inertial effects may contribute to net changes in body orientation. Finally, accurately separating changes in orientation due to wing inertia from those due to aerodynamic forces requires higher resolution kinematics than were recorded in this study. Therefore, we reduced the roll record for each turn to a single periodic function, discarding the variation in roll that occurred during each wingbeat but accurately capturing the whole-turn rates of change in roll and roll velocity. In cockatiels, roll acceleration was significantly correlated with asymmetries in wing stroke amplitude in the world coordinate system, whereas roll velocity was significantly correlated to wing stroke amplitude asymmetries in the body coordinate system. In both cases, this reflects a larger downstroke amplitude of the outside wing compared to the inside wing. As has been discussed elsewhere, the simple approach described above was not fruitful in the analysis for the cockatoo turns. Instead, cockatoo roll acceleration was well predicted by a comprehensive blade-element model that incorporated world coordinate system wing velocity, wing position and wing feathering angle.

Examination of the electromyograms recorded from the cockatiel flight muscles showed that asymmetric activation of the left and right pectoralis muscles – the main flight motors – was strongly correlated with roll velocity. The same muscle asymmetry was weakly correlated with the kinematic measure most closely associated with roll velocity, the downstroke wing amplitude asymmetry in the body coordinate system. In the cockatoos, no single electromyogram measure was tightly correlated with changes in roll orientation, but a number of different muscles appear to contribute to different factors related to changes in body orientation.
A. A simple model for avian flapping turns

The cockatiel results provide the outline for a simple model for flapping avian turns. In the first half of the turn, the bird increases the neuromuscular activation delivered to the outside wing pectoralis muscle. Presumably in conjunction with simultaneous increases in the activation of the upstroke musculature, the outside wing flaps through a larger arc than the inside wing in the body coordinate system. However, this larger flapping arc and therefore greater wing velocity lead to an aerodynamic force asymmetry which causes the bird to roll toward the inside of the turn. This rolling motion reduces the world coordinate system velocity of the outside wing while simultaneously enhancing that of the inside wing, leading to a reduction in aerodynamic torque. However, the inward rolling motion established earlier in the wingbeat enhances the amplitude of the inside wing stroke in the world coordinate system, making the original source of the force asymmetry, the outside wing pectoralis, difficult to discern. At the midpoint of the turn the muscle activation patterns reverse, driving roll in the opposite direction. Throughout the turn, peak aerodynamic forces are generated at or near mid-downstroke\(^{16}\), and provide an inward force that is geometrically dependent on roll angle. In the case of asymmetric flapping amplitudes in the body coordinate system, aerodynamic and inertial changes in roll interact additively, with both leading to changes in roll orientation in the same direction.

B. Cockatiels versus Cockatoos

This simple model provides a good explanation for the cockatiel, but not the cockatoo data. Although both species exhibited the same basic relationship between roll and change in heading, the cockatoos’ changes in roll orientation were not easily predicted by simple differences in downstroke amplitude. Instead, a complete blade element analysis of the two wings provided a good prediction of roll acceleration over a single wingbeat (rather than whole turn) period, but required more detailed inputs\(^{5}\). The discrepancy between the cockatoos and cockatiels is likely one of appearances than actual differences. The cockatiels likely also make use of the asymmetries in wing feathering angle and position found in the cockatoos, but such a detailed investigation was not required to predict changes in roll because of the substantial asymmetries in wing stroke amplitude. The cockatoos appear to have experienced some difficulty in navigating the flight course as indicated by their abbreviated upstroke duration, and may have been operating near their muscle force and power limits. This may have inhibited their use of turning mechanisms potentially detrimental to total aerodynamic force production such as the large stroke amplitude asymmetries used by the cockatiels. At faster flight speeds or in shallower turns the cockatoos may make greater use of wing stroke amplitude asymmetries.

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