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Modulation of Flight Muscle Recruitment and Wing Rotation Enables Hummingbirds to Mitigate Aerial Roll Perturbations

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SUMMARY

Both biological and artificial fliers must contend with aerial perturbations that are ubiquitous in the outdoor environment. Flapping fliers are generally least stable but also most maneuverable around the roll axis, yet our knowledge of roll control in biological fliers remains limited. Hummingbirds are suitable models for linking aerodynamic perturbations to flight control strategies, as these small, powerful fliers are capable of remaining airborne even in adverse wind conditions. We challenged hummingbirds to fly within a steady, longitudinally (streamwise) oriented vortex that imposed a continuous roll perturbation, measured wing kinematics and neuromotor activation of the flight muscles with synchronized high-speed video and electromyography and used computational fluid dynamics (CFD) to estimate the aerodynamic forces generated by observed wing motions. Hummingbirds responded to the perturbation with bilateral differences in activation of the main flight muscles while maintaining symmetry in most major aspects of wing motion, including stroke amplitude, stroke plane angle, and flapping frequency. Hummingbirds did display consistent bilateral differences in subtler wing kinematic traits, including wing rotation and elevation. CFD modeling revealed that asymmetric wing rotation was critical for attenuating the effects of the perturbation. The birds also augmented flight stabilization by adjusting body and tail posture to expose greater surface area to upwash than to the undesirable downwash. Our results provide insight into the remarkable capacity of hummingbirds to maintain flight control, as well as bio-inspiration for simple yet effective control strategies that could allow robotic fliers to contend with unfamiliar and challenging real-world aerial conditions.

INTRODUCTION

As flying animals navigate their habitats near the Earth's surface, they contend with complex, unpredictable airflows that challenge their aerial stability. To remain airborne, flapping fliers need mechanisms for rapidly adjusting movements with respect to airflow perturbations [1–3]. Whether active or passive in nature, such mechanisms are likely subject to strong natural selection in biological fliers [4] and are critical for sustained flight in artificial fliers [5].

The literature on responses to gust perturbations and chaotic flow in biological fliers is rich. Prior studies have demonstrated the diverse strategies of insects, despite their small size and limited sensorimotor resources, as compared to vertebrate fliers. Passive mechanisms include self-righting through counter-torque produced by flapping [3] and passive inertial control provided by appendages [6]. Insect flight studies also showcase a wide array of active responses, including changes in stroke amplitude [7], angle of attack (AoA) [6, 8, 9], angular rotation [7], and wingbeat frequency [8]. A particularly impressive example is the ability of hawkmoths to negotiate whirlwind perturbations through drastic stroke-to-stroke alterations of wing kinematics [10]. However, it remains largely unknown how vertebrate fliers, such as birds and bats, combine active and passive mechanisms to contend with aerial perturbations.

Compared to insects, vertebrate fliers have more elaborate nervous systems that may confer greater neuromuscular control of their more articulated wing systems. Bats, for instance, harness inertial effects by asymmetrically folding their wings to