The influence of sensory delay on the yaw dynamics of a flapping insect

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In closed-loop systems, sensor feedback delays may have disastrous implications for performance and stability. Flies have evolved multiple specializations to reduce this latency, but the fastest feedback during flight involves a delay that is still significant on the timescale of body dynamics. We explored the effect of sensor delay on flight stability and performance for yaw turns using a dynamically scaled robotic model of the fruitfly, Drosophila. The robot was equipped with a real-time feedback system that performed active turns in response to measured torque about the functional yaw axis. We performed system response experiments for a proportional controller in yaw velocity for a range of feedback delays, similar in dimensionless timescale to those experienced by a fly. The results show a fundamental trade-off between sensor delay and permissible feedback gain, and suggest that fast mechanosensory feedback in flies, and most probably in other insects, provide a source of active damping which compliments that contributed by passive effects. Presented in the context of these findings, a control architecture whereby a haltere-mediated inner-loop proportional controller provides damping for slower visually mediated feedback is consistent with tethered-flight measurements, free-flight observations and engineering design principles.

Keywords: Drosophila; sensory delay; flapping flight; flight control; insect flight; insect aerodynamics

1. INTRODUCTION

The variety and the complexity of aerial manoeuvres in insect flight have fascinated biologists and aerospace engineers, leading to a concerted effort to understand the aerodynamics of flapping flight as well as how the requisite forces and moments are generated and controlled. Although the use of dynamically scaled robots and computational fluid dynamic studies have led to an understanding of the unsteady mechanisms that explain the elevated gross force production [1–3], the relationship among sensory information processing, wing kinematic changes and aerodynamic force modulations required for performing active manoeuvres and maintaining stable flight remains an active area of research [4–6]. The mathematical and experimental tractability of yaw turns during hovering, along with the vast body of literature regarding visual- and mechanosensory-mediated responses to rotatory stimuli, has made the study of wing kinematics governing such manoeuvres an excellent entry point into the problem [7–10].

Recent studies have highlighted the importance of passive damping in flapping flight as a yaw rate stabilizing mechanism [11,12]. However, the ubiquity of active sensor-based stabilization reflexes in flying animals [13–16], begs the question: what is the relationship between active compensatory feedback and passive counter-torque during flight? One way of exploring the role of active feedback on a flapping system that exhibits passive stability is to take advantage of a special type of robotics, called captive trajectory systems. Captive trajectory systems measure the applied forces on the object of interest, run these forces through the equations of motion, and actuate the body appropriately in real-time under closed-loop conditions. For the study of flapping flight, such a system would entail measuring forces and moments on the airframe of a dynamically scaled robot, integration of the rigid body equations of motion and rotating/or translat-
[11,18–21]. In an effort to construct a linearized state-space model of insect flight dynamics during hovering, a convenient framework for addressing flight control questions, researchers have conducted a system identification of a quasi-steady-based flight simulator [22]. Under quasi-steady assumptions, stroke-averaged yaw torque is expected to be linear with respect to yaw rate [11,12]. This result extends to the unsteady case as shown by studies using dynamically scaled robots [20,21]. Additionally, dynamic system response tests in these robots confirm that a first-order linear stroke-averaged model accurately captures the essential dynamics of the system on timescales larger than a wing stroke for a variety of kinematic control inputs [21].

Feedback delays can induce fundamental performance limits or even destabilize an otherwise stable system. Neural processing delays may, therefore, have a profound impact on the dynamics and control of biological systems. For example, delay plays a crucial role in dictating constraints on the architecture of a stabilizing controller in cockroach wall following [23]. The sensory systems of Drosophila, like other dipterous insects, possess multiple specializations that result in reduced latency and increased temporal resolution. Features of the fly visual system include an elevated flicker fusion frequency, approaching 300 Hz in some cases [24], as well as a unique neural superposition architecture that allows for fast response sensitivity without the normally associated loss in spatial resolution [25]. These factors make for one of the fastest visual systems in the animal kingdom, yet, visual to motor delays are still roughly 30 ms in houseflies [26] and 40 ms in Drosophila [27,28], slower than the timescale of body dynamics during rapid saccades and other flight behaviours [8,29]. Specialized mechanosensory structures called halteres, which are unique to dipterans, evolved from hind wings and provide feedback on a much shorter timescale than is possible with the visual system [7,15,16]. In addition to providing timing input for synchronous flight control muscle [30,31], sensors at the base of the haltere are thought to encode rotation rate by detecting strain induced by Coriolis forces [32,33]. Low latency spike responses to mechanoreceptors [34], and direct electrical synaptic input to steering motor neurons from haltere afferents bypassing the thoracic neuropil [35–37], provide evidence that the haltere-motor pathway is optimized for expediency. In Calliphora, the total sensor to motor feedback delay is estimated to be approximately 3 ms [36,38], or roughly 1/2 a wing stroke period. Given that time constants on the order of three wing beats have been readily observed in the yaw rate body kinematics of fruitflies [8], such delays remain significant and should be handled explicitly in any flight control model [39]. The ability of flies and other insects to navigate and fly stably in the presence of significant feedback delays motivates an in-depth look at the influence these delays have on system dynamics.

In this study, we explored the effect of feedback delay on the stability and performance of a proportional yaw rate controller in the context of a stereotyped body saccade of a fruitfly, in which the animal performs a rapid turn of approximately 90° in 50–100 ms [40,41]. To perform this analysis, we used a dynamically scaled robotic model with captive trajectory capability about the yaw axis. Yaw torque was controlled through a bilateral asymmetry in an angle of attack, which has been observed in yaw turns of real flies and used in previous studies [21,42]. We studied step and impulse responses in yaw velocity with the robot under proportional control for a range of feedback delays similar in dimensionless timescale to those present in the nervous system and compared these responses with stroke-averaged simulations. The results demonstrate that proportional control decreases the system time constant by adding an active damping component, but is constrained by a trade-off between sensor delay and permissible feedback gain. This suggests that the role of the haltere may be to provide fast inner-loop feedback, resulting in additional active damping which would allow the slower visual system to operate at higher gain with a faster response for the same level of robustness. The experiments also provide evidence that the large open-loop responses observed in tethered-flight might not be an artefact of the preparation, as previously suggested [43], but are indeed what would be required of a well-tuned flight control system.

2. MATERIAL AND METHODS

2.1. Robotic fly apparatus

Experiments were conducted in a 1 × 2.4 × 1.2 m tank of mineral oil (Chevron Superla white oil; Chevron Texaco Corp. San Ramon CA, USA; density 880 kg m−3, kinematic viscosity 115 cSt at 25°C) using a dynamically scaled model of Drosophila with hardware identical to the apparatus described previously [21]. We will briefly reiterate this description for convenience as well as highlight the additional capabilities enabled by a software redesign. The robot consists of two isometrically scaled acrylic wings (length (l) = 230 mm, mean chord (c) = 65 mm and width = 2.3 mm), each with three independently actuated degrees of freedom: stroke angle (Φ), deviation angle (θ) and rotation angle (α), as illustrated in figure 1a. The stroke axes of the two wings were parallel and separated by 0.11 m. The wing motor assemblies were attached to a common frame that was mounted on a shaft to allow rotation about the functional yaw axis. A geometrically scaled body model was not used because the damping owing to the body is roughly two orders of magnitude smaller than that of the flapping wings, and can be ignored for most studies [11,12,21]. The stroke position of each wing was controlled by a stepper motor (M-1715-1.5D, Schneider Electric Motion, Marlborough, CT, USA), whereas the rotation and deviation positions were controlled by digital servo motors (HSC-5996TG, Hitec RCD, Poway, CA, USA). The yaw rotation of the airframe was actuated by a stepper motor (M-2218-3.0S, Schneider Electric Motion, Marlborough, CT, USA). A torque sensor (TQ202-25Z, Omega Engineering, Stamford, CT, USA; full-scale range of 0.175 N-m, accuracy of 0.2% full-scale output) mounted axially between the shaft and base plate measured yaw torque in the body frame.
The robot was controlled using a computer running a hard real-time Linux kernel with custom software written in Python and C. At each time step within a 3 kHz real-time loop, torque generated by the aerodynamic forces on the wings was measured and passed to a model of the fly’s inertial dynamics and new wing kinematics were generated based on a prescribed output-feedback controller. The state variables were held in a buffer in order to implement a virtual sensor delay. The model of the fly’s inertial dynamics is given by:

\[ \dot{c} = v \left[ 2 \cdot 1 \right] \]

\[ I \dot{v} = \tau_{\text{meas}}(t) - b \omega \approx \tau_{\text{meas}}(t), \]  

where \( c \) is the heading angle, \( I \) is the moment of inertia about the yaw axis, \( \omega \) is the yaw velocity, \( \tau_{\text{meas}} \) is the yaw torque measured by the sensor and \( b \) is a velocity-dependent body damping term. This equation was integrated using the classical Runge–Kutta method [44] to set the yaw velocity and heading angle of the system at each time step. For the experiments in this manuscript, the body damping term was dropped for the same reason that a physical body model was not used; the aerodynamic forces acting on flapping wings that provide damping during yaw rotation dominate the effects of body drag [11]. For appropriate dynamic scaling of this equation, we matched the Reynolds number (re), dimensionless yaw velocity (\( \omega^* \)) and dimensionless moment of inertia (\( I^* \)). These dimensionless quantities are defined by the following:

\[ Re = \frac{2R \rho f \bar{c}}{v}, \]  

\[ \omega^* = \frac{\omega}{f} \]  

Figure 1. Experimental design. (a) Design drawing of the dynamically scaled robotic model. Each wing has three degrees of freedom, stroke, deviation and rotation. Torque is measured where the base of the yaw rotation shaft meets the airframe. (b) Pictorial representation of the wing kinematics, illustrating the asymmetry in wing rotation angle consistent with the differential angle of attack deformation mode described in Dickson et al. [21]. (c) Block diagram model used for stroke-averaged simulations of a proportional yaw rate controller. The model has set point of zero and a commanded asymmetry input representing a motor command to the steering muscles. The two saturation blocks are a morphological limit on the maximum asymmetry and a saturation in the drag coefficient approximated by a hyperbolic tangent function with one measured parameter. \( C_u \) is the actuation coefficient, \( C_v \) is the damping coefficient and \( u \) is the asymmetry parameter. There is a fixed sensor delay, \( \delta \), in the feedback loop. (d) Sample data for a typical step response experiment. The kinematics shown are the stroke angle (single blue curve) and the left (red) and right (blue) wing rotation angles. The commanded asymmetry in rotation angle is in red while the actual asymmetry is in blue. The bottom panel is the corresponding yaw rate response.

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\[ \omega^* = \frac{\omega}{f} \]  

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where $R$ is the wing length, $\Phi$ is the (peak-to-peak) stroke amplitude, $f$ is the flapping frequency, $\bar{c}$ is the mean wing chord, $\nu$ is the kinematic viscosity and $\rho$ is the density of the fluid. A flapping frequency of 0.167 Hz was used to yield a $Re$ of 100, consistent with flapping flight in Drosophila [45]. The dimensionless moment of inertia about the functional yaw axis used in this study was $1.97 \times 10^3$, in agreement with those used in previous studies [12,21]. This was calculated by modelling the fly as a cylinder inclined at $55^\circ$, corresponding to a hovering flight posture. All subsequent values and equations will appear in their dimensionless form.

2.2. Kinematics

We used idealized Drosophila wing kinematics that use a differential angle of attack control mode as described previously [21]. The linearity of additional control modes studied in previous work allows us to perform these studies in the context of just one mode and apply the results generally to a desired superposition of control modes [21]. The kinematics consist of a nominal set based on previous work [46], augmented with an asymmetry parameter in right and left wing rotation angle as a means of generating yaw torque. The stroke position, deviation and rotation angle for the baseline kinematics are given as follows:

$$
\phi_0(t) = \frac{\Phi}{\sin^{-1}(k_b)} \sin^{-1}[k_b \cos(2\pi ft)],
$$

$$
\theta_0(t) = 0,
$$

and

$$
a_0(t) = \frac{a_0}{\tanh(k_b)} \tanh[k_b \sin(2\pi ft)],
$$

where $f$ is the flapping frequency, $\phi_0$ is the stroke amplitude, $a_0$ the rotation amplitude and the parameters $k_b$ and $k_c$ control the shape of the wing kinematics. Values of $k_b = 0.01$ and $k_c = 1.5$ were selected to produce waveforms that resemble an idealized version of the wing kinematics of Drosophila [21,46]. Similarly, a value of $\phi_0 = 70^\circ$ was used to generate a peak-to-peak stroke amplitude of $140^\circ$ and a value of $a_0 = 45^\circ$ was used to give a $45^\circ$ angle of attack at midstroke. Because the yaw rotation axis is aligned with the stroke plane normal and no deviation is considered, the geometric angle of attack is specified by the rotation angle with an appropriate offset. The differential angle of attack mode deforms the baseline rotation angles in the following manner, leaving the other degrees of freedom unchanged:

$$
a_{L,R}(t) = a_0(t) \pm u,
$$

where $u$ is the deformation parameter. A non-zero value for $u$ introduces asymmetry into the wing kinematics, as shown by example, left and right wing tip trajectories in figure 1b. For illustrative purposes, consider a baseline angle of attack at mid-stroke of $45^\circ$. A positive $u$ would increase the rotation angle on the downstroke in the left wing, reducing the angle of attack and consequently the drag force while having the opposite effect on the right wing. This asymmetry would reverse on the upstroke, resulting in a net yaw torque and inducing a turn to the right.

Feedback control was enabled by generating the kinematics from within the real-time loop with a state-dependent differential angle of attack deformation parameter. We implemented a simple yaw rate proportional controller with a zero set point and feed-forward asymmetry, $u_f$, by constructing $u$ in the following manner:

$$
u(t) = -k_p \omega(t) + u_f(t),
$$

where $k_p$ is the proportional feedback gain and $\omega$ is the yaw rate. The effect of each term in the controller is apparent in the sample step response shown in figure 1d. When considering feedback with a fixed delay this becomes:

$$
u(t) = -k_p \omega(t - \delta) + u_f(t),
$$

where $\delta$ is the delay time. A morphological limit on the maximum asymmetry was also considered, and manifested as a software limit on the maximum value of $u$.

2.3. Stroke-averaged modelling

Simulations were carried out with code written in Python that used the SciPy module [47] by considering the following stroke-averaged linear dynamics:

$$
i \omega = \tau_\omega + \tau_u = -C_u \omega + C_u u(t),
$$

where $\tau_\omega$ and $\tau_u$ are the contributions to dimensionless torque from passive damping and the asymmetry parameter, $u$, respectively; $C_u$ is the damping coefficient and $C_u$ is the actuation coefficient. The dimensionless damping coefficient and dimensionless actuation coefficient were both experimentally determined by averaging yaw torque over five identical wing strokes, as measured by the robotic fly apparatus, following a similar procedure to that described previously [21]. These measurements were performed with prescribed yaw velocity in the absence of the captive trajectory system. The dimensionless damping coefficient used was $7.47 \times 10^3$ and was determined by a linear fit of the relationship between stroke-averaged yaw torque and yaw rate for a fixed value of $u$. The dimensionless actuation coefficient was $3.53 \times 10^1$ and was derived from the linear relationship between yaw torque and the actuation parameter for a fixed yaw rate.

In addition to including the constraint on the maximum value of $u$, we also modelled a saturation in the actuation torque, $\tau_u$. Whereas the drag coefficient for a revolving wing in a Reynolds number regime near 100 is relatively linear with rotation angles near $45^\circ$, this approximation breaks down with significant deviation in rotation angle which spawns the saturation in the actuation torque. The saturation was modelled with a hyperbolic tangent function with one experimentally determined parameter, $A$:

$$
\tau_u = \frac{1}{A} \tanh(Au) C_u.
$$

The experimental parameter had a value of $A = 1.39$, and was determined by least-squares fit of equation (2.13) to torque versus $u$ data for a fixed yaw velocity.
The dynamics in equation (2.12) can be written as a transfer function and combined with both the saturation in equation (2.13) and the controller in equation (2.11) to form a block diagram model of the system used to perform the simulations as illustrated in figure 1c.

3. RESULTS

3.1. Step responses in the undelayed system

The role of feedback gain in determining the system time constant was explored through a series of yaw velocity step response experiments. The step was approximated by a steep ramp and hold of the feedforward command parameter, $u_{ff}$, with the ramp width equal to 0.20 wing strokes and temporally centred on the defined trial start time, $t = 0$. All trials were conducted in closed-loop with undelayed feedback and consisted of 5 wing beats that were bilaterally symmetric (i.e. $u_{ff} = 0$) to produce fluid conditions representative of hover, followed by 10 wing beats to measure the system response to a change in the commanded input. Illustrative sample data for these trials are shown in figure 1d. The controller gain, $k_p$, was varied from 0 to 0.93. Higher gains were not possible because they would lead to wing kinematics that were both biologically implausible and beyond the calibration limits of the servo motors controlling rotation. A proportional controller leaves a steady-state error that is gain-dependent, meaning that controlling rotation.

Higher gains were not possible because they would lead to wing kinematics that were both biologically implausible and beyond the calibration limits of the servo motors controlling rotation. A proportional controller leaves a steady-state error that is gain-dependent, meaning that controlling rotation. Although the magnitude of the step change in velocity would not affect the time constant for a linear system, we felt a more relevant comparison was to choose $u_{ff}$ for each trial in a manner that resulted in a consistent steady-state yaw velocity of 27° stroke$^{-1}$, a conservative upper limit on the peak speed during a saccade [8,40].

Time-series data for the yaw rate step responses of the robot are shown in figure 2a. The response is indicative of an approximately linear first-order system, with higher frequency oscillations, owing to torque peaks generated over each half-stroke, superimposed on the response. We determined the time constant of each response by a least-squares fit of a first-order response to the trace. Time constants for each controller gain are plotted in figure 2c with a comparison with model predictions. The time constant decreased with gain at a diminishing rate, in close agreement with model predictions.

High gain cases in which sub-wingstroke time constants were achieved, resulted in angle of attack asymmetries (figure 2b) that are much larger than those observed in Drosophila during high-speed video sequences in free-flight [8,42]. We conducted a second set of step response experiments that were more in line with observations of real flies by imposing a 10° limit on the angle of attack asymmetry. These data are shown alongside their corresponding system time constants in figure 2d–f. The morphological limit on the angle of attack asymmetry reduced the impact of controller gain, producing an asymptotic floor in the system time constant.

3.2. Stability in the delayed system

To examine the destabilizing effect of sensor delay, we conducted impulse response experiments for four values of feedback delay, spanning the range of relevant delays expected in a fly. The four feedback delays we considered were 0.5, 1, 5, and 10 wing strokes, with the range of controller gains used for each delay chosen based on simulation results. For each delay, we measured the response to a modified impulse in $u_{ff}$ for a series of gains to determine the gain at which the system becomes unstable. The modified impulse consisted of a positive step in $u_{ff}$ using the same approximation for a step function as in the previous set of experiments, followed by a corresponding negative step after a duration of 4.0 wing strokes. We fit a harmonic function with a hyperbolic tangent amplitude-envelope to the yaw rate time-series data following the termination of the impulse by optimizing a least-squares cost function. The asymptotic nature of the amplitude was used to determine the stability of each trajectory. The time-series data are shown for the five wing beat delay case in figure 3a to illustrate the method of finding the gain value at the stability transition. The yaw rate data display a characteristic oscillatory behaviour with a period that is relatively independent of gain. The amplitude of the oscillation decays to zero for stable cases and grows towards a limit cycle for the unstable cases. The trials with other delays yielded similar results with different periods of oscillation and limit cycle amplitudes. The stability transition gain is plotted in figure 3b with a comparison with model predictions. The results indicate a fundamental trade-off in permissible gain and delay for gains above a certain threshold. For gains below this threshold, the system appears to be stable regardless of delay.

3.3. Step responses in the delayed system

Even at gains below the stability curve, sensor delay can have detrimental effects on system performance. Following the same protocol as used in the step response experiments for the undelayed system, we conducted trials with the same four feedback delays of interest as the impulse response trials. The range of controller gains used for each delay spanned the neighbourhood of a critically damped response. The gain values were once again chosen based on simulation results. With sufficient feedback gain, sensor delay introduces ringing in the step responses which is characteristic of systems of second order and higher (figure 4a). Per cent overshoot of the steady-state yaw velocity was used as a performance metric and is plotted against controller gain in figure 4b for the one-wing stroke delay case. The 5 per cent overshoot gain was estimated by spline interpolation of the overshoot curve and is shown as a function of delay and compared with simulation results in figure 4c. The gain–delay curve exhibits a similar trade-off as in the stability case, but without a gain threshold. For large enough delay, the system appears underdamped even for an arbitrarily small gain.

The data deviated noticeably from the stroke-averaged model predictions during the initial overshoot. We attributed this discrepancy to the oscillation in yaw...
velocity at wing beat frequency that was superimposed on the largely second-order step response. The phase relationship of the wing beat frequency oscillation with the time of the peak in the step response could cause a systematic overestimate or underestimate, because phenomena within an individual stroke obviously cannot be resolved in a stroke-averaged simulation. As a check of this hypothesis, we adjusted the phase of the step change in the asymmetry parameter relative to the wing beat cycle to show this could account for the observed variation and the dominant dynamics remained unchanged.

4. DISCUSSION
The results of this study highlight the importance of explicitly addressing the impact of delay when modeling the flight control system in Drosophila and other insects. Despite the open-loop yaw velocity dynamics...
being passively stable [11,12,20,21], time delays consistent with those present in a fly’s nervous system are sufficient to destabilize the closed-loop system for high enough gain. This system instability was observed even when only subjected to inherent process noise and not given a commanded input, \( w_i \) (figure 5). Introducing proportional control reduces the system time constant by adding an active damping component (figure 2). For the undelayed case, this effect is limited only by the saturation of the actuation torque and any morphological limit on the asymmetry in angle of attack. For delayed feedback, the length of delay places fundamental limits on the controller bandwidth and likewise on the permissible gain. Measured responses to a modified impulse function provided a consistent means of identifying the region of gain–delay space in which the system is stable. In addition, these experiments revealed an asymptote in the gain–delay curve that provides a threshold below which the system is stable regardless of delay. However, even if the system is stable, additional delay can accrue important performance deficits. Step responses in the delayed system with sufficiently high gain displayed undesirably large amounts of overshoot and ringing, indicative of severely underdamped systems of second order or higher. For longer delays, this behaviour was unavoidable even with minimal feedback gain.

### 4.1. Active damping

Recent studies have suggested that the angular deceleration phase of yaw turns in flying animals is entirely mediated by passive damping [12]. The authors make the argument for passive deceleration based on a comparison of published data with two separate hypotheses: a passively damped model and an active model whereby asymmetric flapping generates constant braking torque. The passive model predicts an exponential decay in yaw rate, similar to real trajectories, whereas the active constant torque model predicts a linear decay. Dynamically scaled robotic experiments and computational methods have shown that aerodynamic damping in flapping flight is indeed important to the dynamics of yaw turns [11,20,21]. In addition, these studies showed that the resulting passive dynamics are approximately first order and linear in rotation rate, which would lead to the observed exponential decay. However, the existence of strong compensatory reflexes in flies that depend on the magnitude of the stimulus would suggest that these insects use active stabilization that may be approximated by proportional feedback [14,17]. As is evident from the time-series step response data, as well as an analysis of the stroke-averaged equations, a proportional feedback controller would also exhibit exponential decay. Thus, the existence of an exponential decay in yaw rate cannot be taken as evidence for the absence of active feedback. Consider the transfer function for the closed loop dynamics of the linear stroke-averaged model under proportional control, \( G(s) \):

\[
G(s) = \frac{k_p C_u}{Is + C_u + k_p C_u} = \frac{k_p C_u}{Is + C_u}. \tag{4.1}
\]

The characteristic equation for the closed-loop system has the same form as the process dynamics with an effective damping of \( C_w = C_u + k_p C_u \). In a stroke-averaged sense, proportional feedback decreases the time constant of the system by providing an active form of damping.
Flies, like most animals, use a combination of feedforward motor programmes and both neural and mechanical feedback during locomotion [48]. Given the relatively short time course associated with saccades, there is some question as to whether or not the feedback component is involved at all during such manoeuvres [41]. Drosophila exhibit strong visual- and haltere-mediated equilibrium reflexes to rotational stimuli [7,15,49,50], providing some evidence for respective feedforward mediation of saccade dynamics, whereas visual feedback plays little or no role subsequent to the initiation [41]. Researchers conducting free-flight studies of mechanically induced yaw perturbations concluded the feedback signal from the haltere was used to generate reflexive course corrections, but the animals did not use active braking during the perturbation or at the termination of the compensatory manoeuvre [7]. In light of the potential implications of sensory delay on an actively controlled deceleration, it may even seem prudent for animals to perform these fast manoeuvres in open-loop. However, feedback systems are ubiquitous across biological systems and engineering applications alike, presumably because they provide robustness to uncertainty. Whereas the term robustness has very specific connotations in control systems, anecdotal observations of fruitflies convey the general concept of their ability to handle external perturbations, uncertain process dynamics and internal asymmetries. Drosophila are able to regulate yaw torque with partial wing ablations, artificially added wing mass and many other manipulations [41]. Further, the moment of inertia of a fruitfly provides the condition for critical damping:

\[ k_{\text{critical}} = \frac{6I + C_u \delta - 4\sqrt{(2I + C_u \delta)}}{C_u \delta}. \]  

(4.3)

Requiring the poles to reside in the left half-plane yields the condition for stability:

\[ k_{\text{stable}} \leq \frac{2I + C_u \delta}{C_u \delta}. \]  

(4.4)

Equations (4.3) and (4.4) provide reasonable approximations of the experimentally determined gain–delay curves. In the limiting case of zero delay, all timescales are long relative to the delay, allowable gain goes to infinity, and we recover the undelayed closed-loop dynamics. Examining equation (4.4) reveals the source of the stability threshold in gain, leading to a sufficient condition for stability:

\[ k_p \leq \frac{C_u}{C_u}. \]  

(4.5)

The same asymptote appears to exist for critical damping, contrary to the experimental results. However, this is an artefact from the breakdown in our approximation for delay at long delays relative to the dynamics. To show that equation (4.5) is still relevant for the stable gain case, we consider the loop transfer function, \( L(s) \), with the full expression for delay:

\[ L(s) = \frac{k_p C_u e^{-s\delta}}{Is + C_u}. \]  

(4.6)

We assess the stability of the closed-loop system by applying the Nyquist criterion. With the condition on \( k_p \) given by equation (4.5), the H-infinity norm is less than one, which guarantees stability but is not particularly useful for most performance metrics. The stability threshold in gain, therefore, results from the strength of passive damping relative to disturbances from a delayed control input.

On sufficiently long timescales relative to the delay, equations (4.2–4.5) provide a valid description of the dynamics and we may use them to compute an effective damping similar to the undelayed case. The relevant term is the real part of complex conjugate poles in \( G_d(s) \), equation (4.2), which gives the decay rate. Normalizing by the moment of inertia gives the effective damping:

\[ C_u = \frac{2I + (C_u - k_p C_u) \delta}{2\delta}, \]  

(4.7)

which is relevant for gains near \( k_{\text{critical}} \). Shorter delay allows for larger effective damping and a faster system response.
4.3. Performance limits

Time delays impose fundamental limits on the performance of the closed-loop system which may be analysed using the crossover frequency inequality [39]:

$$- \arg P_{ap}(iw_{gc}) \leq \pi - \phi_m + \eta gc \pi / 2 = \phi_v,$$  

(4.8)

where $P_{ap}(s)$ is the all pass system containing the non-minimum phase portion of the loop transfer function, $w_{gc}$ is the gain cross-over frequency, $\phi_m$ is the desired phase margin, $\eta gc$ is the slope of the gain curve at cross-over and $\phi_v$ is admissible phase lag in the minimum phase component of the dynamics. Decomposing equation (4.6) and applying equation (4.8) we get the following condition on $w_{gc}$:

$$w_{gc} \leq \delta \phi_v,$$  

(4.9)

meaning that time delay limits the maximum permissible cross-over frequency and longer time delays impose more restrictive conditions. This results in an expression for gain for a desired level of phase margin, $k_{\phi_m}$:

$$k_{\phi_m} = \sqrt{\frac{(\pi - \phi_m + \eta gc \pi/2)^2 I^2 + C_0^2 \delta^2}{C_0^2 \delta^2}}.$$  

(4.10)

A large cross-over frequency is desirable both for controller tracking and load disturbance rejection at higher bandwidth and is facilitated by high gain. Longer delay with the same amount of phase margin demands a lower cross-over frequency. Delay, therefore, dictates the nature of the trade-off between robustness and response time.

4.4. Visual and mechanosensory feedback integration

There is strong anatomical and physiological evidence that suggest the primary flight control sensors for detecting yaw rate in flies, namely the vision system and the halteres, have evolved under selective pressure to reduce latency [25,36,37]. This idea is consistent with the tangible fitness associated with performance limits imposed by sensory delays. The specializations in flies’ sensory systems may facilitate their high performance behaviour [13]. Tethered-flight experiments offer a method to decouple and systematically measure visual and mechanical gain, but have often been criticized for producing exaggerated responses compared with similar disturbances in free-flight [43]. We will look at the open-loop responses to visual and mechanical yaw velocity stimuli in the context of our results and provide a potential reconciliation of the observed open-loop responses with free-flight yaw dynamics.

Previous studies of tethered Drosophila measured bilateral difference in wing beat amplitude (ΔWBA) tuning curves independently for visual and mechanical yaw velocity stimuli [16]. Using a calibration of ΔWBA to yaw torque of 9.36 $\times$ 10^{-9} NmV^{-1}, estimated from data in another study using the same wing beat analyser instrument [51], we obtain a crude estimate for haltere and visual feedback gain. Direct torque measurements in response to visual stimuli performed in an earlier study provide some independent confirmation of this estimate [52]. For mechanical stimuli, yaw torque was approximately linear with yaw rate, with a slope consistent with a proportional controller of $k_v = k_{\text{haltere}} = 0.6$. This estimate of gain comes from the non-dimensionalized slope of regressed mechanical response data [16], multiplied by the torque calibration constant and normalized by $C_v$.

Given the estimated feedback delay of the haltere, this gain is in close agreement with what would be expected for a proportional controller conforming to traditional control systems design criteria. The estimated haltere-based controller falls between the 75° and 45° phase margin lines, given by equation (4.10), on our gain–delay plot in figure 6a. With the longer delay associated with the visual system, one might expect the gain to be much smaller in the visual system. However, over the region where the visual response is proportional to the stimulus, the gain is actually much larger with $k_v = k_{\text{visual}} = 12.2$, which would be remarkably unstable according to our results. The important features of the visual response that this neglects is the roll-off that occurs at roughly $w_v = 0.7$ Hz and the influence of haltere feedback on the dynamics. A better interpretation of a visually mediated yaw controller is a low-pass filter. We estimate the controller transfer function to be:

$$C_{\text{visual}} = \frac{k_{\text{visual}} w_v}{s + w_v}.$$  

(4.11)

For short delays, such as a feedback loop from the haltere, the permissible cross-over frequency is larger than the process pole, meaning that large steady-state gain and small tracking error over low frequencies can be achieved with a simple proportional controller. For the visual system, the permissible cross-over frequency is smaller than the process pole, which in this case necessitates the addition of a low-frequency pole. A low-pass filter provides the most basic implementation of this requirement. If we consider the controller in equation (4.11) applied to the passive dynamics, the steady-state gain is too high and the resulting system is still unstable (figure 6b). However, the haltere delay is small on the timescale of the visual system and proportional feedback from the haltere would provide active damping. The plant dynamics to consider for the visual system would have an effective damping computed from the estimated haltere gain and delay using equation (4.7). The resulting system is stabilized and has good performance characteristics (figure 6b).

Fast, unstable process poles require a higher cross-over frequency to control them. Since the permissible cross-over frequency for the visual system is smaller than the process pole, the process dynamics are required to be stable. The passive dynamics in yaw velocity are already stable. Added effective damping from a haltere inner feedback loop is, therefore, not necessary for stability, but does allow the visual system to operate at higher gain with faster response for the same level of robustness. It is conceivable that flies could have visually controlled stable yaw dynamics in the absence of halteres with either larger passive damping or lower visual gain. Hind wings would presumably provide
larger passive damping, whereas low-latency rate sensors given by halteres would allow for a larger amount of active damping. The conservation of overall damping characteristics may very well have paved the way for the evolution of the haltere from the hind wing.

A yaw rate stabilization reflex consisting of an inner-loop proportional controller from haltere feedback that provides effective damping for an outer-loop visual low-pass filter is consistent with open-loop measurements in tethered flight and provides performance and robustness characteristics expected by engineering design principles. In addition, the low cut-off frequency of the visual system, which is necessarily low owing to the permissible cross-over frequency resulting from the visual system delay, explains why visual responses during saccades and other fast manoeuvres are not prominent. A block diagram illustrating the control architecture is shown in figure 6c.

Figure 6. Estimated feedback gain and delay properties for Drosophila in relation to theoretical stability and performance boundaries for proportional feedback from (a) the haltere and (b) a visual feedback low-pass filter with inner-loop haltere-mediated effective damping. Data points (black) are estimated from published data [16,51]. Theoretical stability curves are shown in solid red and the $60^\circ \pm 15^\circ$ phase margin region computed from equation (4.10) is shaded in grey. The dashed red line in (b) gives the stability curve for the visual feedback without active damping. (c) Block diagram of proposed yaw rate control architecture.

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