Complementary feedback control enables effective gaze stabilization in animals

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Visually active animals coordinate vision and movement to achieve spectacular tasks. An essential prerequisite to guide agile locomotion is to keep gaze level and stable. Since the eyes, head and body can move independently to control gaze, how does the brain effectively coordinate these distinct motor outputs? Furthermore, since the eyes, head, and body have distinct mechanical constraints (e.g., inertia), how does the nervous system adapt its control to these constraints? To address these questions, we studied gaze control in flying fruit flies (Drosophila) using a paradigm which permitted direct measurement of head and body movements. By combining experiments with mathematical modeling, we show that body movements are sensitive to the speed of visual motion whereas head movements are sensitive to its acceleration. This complementary tuning of the head and body permitted flies to stabilize a broader range of visual motion frequencies. We discovered that flies implement proportional-derivative (PD) control, but unlike classical engineering control systems, relay the proportional and derivative signals in parallel to two distinct motor outputs. This scheme, although derived from flies, recapitulated classic primate vision responses thus suggesting convergent mechanisms across phyla. By applying scaling laws, we quantify that animals as diverse as flies, mice, and humans as well as bio-inspired robots can benefit energetically by having a high ratio between head, body, and eye inertias. Our results provide insights into the mechanical constraints that may have shaped the evolution of active vision and present testable neural control hypotheses for visually guided behavior across phyla.

Drosophila | active vision | motor control | neuromechanics | fly flight

In most animals, vision is an active process in which muscles move the eyes, head, and/or body independently to direct gaze (1). When animals direct their gaze, how do they coordinate each motor system? In principle, the eyes, head, or body alone could be used to control gaze, but animals generally use a combination of all three during free behavior (2). A central challenge in understanding how the brain controls movement is that animals can coordinate many biomechanical degrees of freedom (DOFs) to achieve a task. Since the eyes, head, and body have overlapping DOFs, how does the brain effectively coordinate all three motor outputs? Furthermore, since the eyes, head, and body have distinct mechanical constraints (e.g., inertia and range of motion), how does the nervous system adapt its control to these constraints? One possibility is that gaze coordination follows a strategy akin to optimal control in engineering, which posits that the nervous system searches for a control strategy to achieve the best possible performance (e.g., high accuracy and speed) while also minimizing a cost such as energy expenditure (3). Revealing the mechanisms that govern the control of gaze across multiple motor outputs can provide critical and unique insights into active vision across phyla.

An interesting possibility is that the neural control of vision is tuned to the corresponding mechanics of each individual motor system. For example, human eye inertia is approximately four orders of magnitude lower than head inertia, so eye movements alone could enable rapid redirection of gaze while minimizing mechanical energy (4). Therefore, from an energy standpoint, it would be beneficial for eye movements to be weighted more heavily when stabilizing or tracking quickly moving features. Mechanisms of gaze control in animals are likely closely related to these mechanical constraints; however, this has not been explicitly demonstrated. In vertebrates, the onset of terrestriality is associated with an increase in eye size and neck mobility (5). This adaptation conferred the ability to direct gaze independent of body orientation, presumably saving considerable energy (6). There is also the intriguing possibility that eye-head-body gaze coordination strategies across phyla show characteristics of convergent evolution—wherein we see similar coordination patterns in organisms with distinct evolutionary histories (2, 7). We hypothesized that the control of gaze in animals is tied to mechanics and having a fast, low-inertia motor to shift gaze (e.g., via the eyes) increases task performance while minimizing mechanical energy expenditure.

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We studied this problem in flying fruit flies (Drosophila melanogaster), which control gaze comparably to primates by combining head and body movements (8, 9). However, the precise control and weighting of motor outputs (head and body) to direct gaze in flight is not well understood. Our previous work showed that head movements coordinate the wings, but the coordination between the head and body remained obscured (10). Here, we go substantially further by including Newtonian mechanics, thereby revealing the neuromechanical and energetic basis of gaze control in flies. Our control model recapitulates classic primate head-eye responses, suggesting convergent gaze coordination mechanisms. Furthermore, the consistent morphological scaling of gaze systems (i.e., large body, small head, and smaller eyes) in many species supports the notion that animals leverage inertial differences to save mechanical energy and maintain adequate performance (11). Our results provide a mechanism by which gaze control minimizes mechanical energy expenditure and maximizes task performance in visually active animals.

Results

Head and Body Movements Are Tuned to Distinct Image Motion Frequency. To reveal the interactions between head and body movements in fly flight, we studied the yaw gaze stabilization reflex with a free pivot tether (Fig. 1 A and B). In this paradigm, the head is unrestrained and the body is free to move about the vertical yaw axis. We modeled the gaze stabilization system as a single-input-multiple-output system, whereby head and body movements combine to stabilize gaze (Fig. 1A and SI Appendix, Fig. S1). Within a virtual reality system, we prescribed external image rotation which elicited a gaze stabilization reflex as flies attempted to minimize retinal image velocity (Fig. 1B). Flies responded to visual rotation by modulating both head and body movements (Fig. 1C). To examine the relative contributions of the head and body to gaze stabilization, we presented flies with visual stimuli consisting of linear combinations of sinusoids (see Materials and Methods) (Fig. 1 C and D). Flies likely experience in natural, free flight about yaw (12, 13).

Using frequency domain system identification techniques (see Materials and Methods), we quantified empirical closed-loop frequency response functions (FRFs) of the head and body separately. The closed-loop FRFs describe the relationship between the visual stimulus (R) and the motor output (head or body) as a function of stimulus frequency or speed (Fig. 1 A and SI Appendix, Fig. S1). For example, the closed-loop FRF for the body is defined as the transformation between the stimulus and the body response and is denoted as B → R. To represent the FRFs mathematically, we defined the closed-loop transforms of the head and body based on our putative control

![Fig. 1](https://example.com/fig1.png)  
**Fig. 1.** Flies control gaze by combining head and body movements. (A) Proposed control framework for gaze stabilization in flies. The fly's gaze (G) is controlled by the sum of body (B) and head (in body reference frame; H) movements. Flies control gaze such that the visual stimulus is shaped into an error signal (E), which is measured by the visual system. Flies aim to minimize the error by sending torque control signals from the body and head neural controllers (Cbody and Chead) to the wing and neck muscles. The control signals drive a compensatory response through the mechanics and aerodynamics associated with the head and body/wings (Pbody and Phead). (B) Illustration of the magnetic tether system and flight simulator. Flies are glued to a magnetic pin and suspended between two magnets, which constrain body movements to rotation in yaw. We used a LED display to visually rotate a grating around the global coordinate frame. (C) The mean time-domain response of the body and head in response to a sum-of-sines visual stimulus. Shaded region: ±1 SD (n = 10 flies). (D) The mean frequency domain magnitude of the body and head in response to the same sum-of-sines stimulus in (C) (n = 10 flies). For visual clarity, only the response at the frequencies present in the sum-of-sines stimulus are shown for the head and body.
model of gaze stabilization (Fig. 1A and SI Appendix, Fig. S1) as:

\[ H_{\text{body}} = \frac{P_{\text{body}} C_{\text{body}}}{1 + P_{\text{head}} C_{\text{head}} + P_{\text{body}} C_{\text{body}}} \]  

and

\[ H_{\text{head}} = \frac{P_{\text{head}} C_{\text{head}}}{1 + P_{\text{head}} C_{\text{head}} + P_{\text{body}} C_{\text{body}}} \]

where \( P_{\text{body}} \) and \( P_{\text{head}} \) are the passive mechanics, or plant, of the body and head, respectively, and \( C_{\text{body}} \) and \( C_{\text{head}} \) are the corresponding neural controllers. When appropriate, we omit the complex frequency \( s \) for clarity.

The closed-loop head and body responses exhibited complementary tuning across visual motion frequency (Fig. 2). We used gain, phase difference, and compensation error as metrics to quantify the difference in tuning. Gain represents the ratio of magnitudes between the visual stimulus and motor outputs, phase difference describes the relative timing, and compensation error describes the normalized magnitude of the generated error signal. Compensation error values near zero indicate ideal performance, values between zero and one indicate improved but not ideal performance, values of one indicate little effect of the head/body on gaze stabilization, and values greater than one indicate that head/body movements have a deleterious effect (see Materials and Methods). Notably, the body response minimized low frequency visual motion whereas the head response minimized high frequency visual motion, thus acting complementarily (Fig. 2 A and B). When considering compensation error, the body operated with low error for frequencies below 1 Hz, indicative of robust gaze stabilization (Fig. 2A). However, compensation error quickly increased after 1 Hz, and had a deleterious effect on gaze stabilization above 3 Hz, suggesting that flies might be better off not moving their body at all in this higher frequency band (Fig. 2A). The head displayed a complementary tuning to the body by reducing compensation error at higher frequencies. From this analysis, we defined body-dominant and head-dominant frequency bands by finding the cross over frequency where head movements improved stabilization (∼2.5 Hz; Fig. 2A compensation error). These results suggest that the nervous system relays low- and high-frequency visual motion differently to the head and body.

**Head and Body Movements Are Complementary to Enable Broadband Gaze Stabilization.** We demonstrated that head and body movements are tuned to distinct frequency bands, but what does this indicate for the performance of the coupled system (head + body)? To understand how head and body movements influence gaze stabilization performance, we computed the FRF for the fly’s gaze or head in the global reference frame (Fig. 1A). The closed-loop gaze transform can be represented mathematically as (SI Appendix, Fig. S1):

\[ H_{\text{gaze}} = \frac{P_{\text{head}} C_{\text{head}} + P_{\text{body}} C_{\text{body}}}{1 + P_{\text{head}} C_{\text{head}} + P_{\text{body}} C_{\text{body}}} \]

The gaze FRF displayed similar gains to the body at low frequencies but starting at ∼2 Hz, head movements began to increase the overall gain (Fig. 2 A and B). For higher frequencies, the gaze gain was determined predominantly by the head (Fig. 2 A and B). Head movements also shifted the overall phase lag closer to zero (Fig. 2 A and B). By fitting a linear model to the phase of the body and gaze response and extracting the average time lag across frequencies, we found that the phase leading head movements reduced the effective latency of the gaze stabilization response by 20 ms (Fig. 2D). The combination of the increased gain and reduced phase lag decreased the overall compensation error (Fig. 2A). Notably, flies operated with compensation error less than one for frequencies up to 12 Hz (Fig. 2A). If just the body was considered, then flies

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**Fig. 2.** Head and body movements combine to enable broadband gaze control. (A) The closed-loop empirical frequency response functions (FRFs) and compensation error for the body (red), head (blue), gaze (purple), and the body of head-fixed flies (orange). The red and blue regions indicate the frequency bands where the body and head dominate gaze stabilization, respectively. The switch between the body-dominant and head-dominant regions was determined by the point where the head response had a smaller compensation error than the body. The overlaid deleterious gray region on the compensation error plot indicates the region where a fly’s response degrades gaze stabilization more so than if the fly simply did nothing. Shaded regions: ±1 STD. (B) The body (red), head (blue), and gaze (purple) time-domain response to single-sine stimuli (gray) at distinct frequencies and amplitudes. Each response in normalized to four cycles of the stimulus presentation. (C) The body-to-head FRF, which quantifies the relative magnitude and phase of the head and body. Black line: grand mean. Gray lines: individual fly means. (D) The time lag fit to the phase response for the head-fixed body, head-free body and gaze computed for the sum-of-sines experiments (for each normalized speed). t test, ***p < 0.001. Head-free: n = 10 flies. Head-fixed: n = 10 flies.
would seem to be operating in a deleterious region for frequencies greater than 3 Hz, but head movements allowed gaze stabilization to remain effective at much higher frequencies. This complementary tuning of head and body movements can be observed on the complex plane, where head and body movements combine (sum of complex responses) to shift the gaze stabilization response closer to perfect compensation and extend the bandwidth of the coupled system (SI Appendix, Fig. S3A). We ensured that this control strategy was maintained for a variety of visual stimuli and was not an artifact of our experimental design (see SI Appendix, Text and Figs. S2 and S3). Thus, head and body movements together enhance gaze stabilization performance.

**Head Movements Are Required for Broadband Gaze Control.**

Our findings establish that head movements are weighted more heavily when compensating for high image velocities, but can the body also fulfill this role? To study if flies could stabilize high-frequency visual stimuli with their body alone, we studied gaze stabilization in head-fixed flies (SI Appendix, Fig. S1). Head-fixed flies did not compensate for the lack of head movements by increasing the gain or phase of body movements (Fig. 2A and Movie S4). The compensation error of head-fixed flies was similar or marginally worse than head-free flies across all frequencies (Fig. 2A). Notably, head-fixed flies were more out of phase and showed an effective gaze latency 20 ms longer than head-free flies, suggesting that not only did flies not compensate for head-fixation but that head-fixation had deleterious effects on downstream wing/body control (Fig. 2A and D) (10). It is possible that flies are not physically capable of applying the amount of torque/power necessary to drive high gain body movements at high frequencies, which would suggest inertial, motor or aerodynamic constraints limit body control. Taken together, our data suggest that body movements are not well-suited for stabilizing high-frequency visual motion.

**Head and Body Movements Are Modulated by Parallel Velocity and Acceleration Sensitive Control.**

Our data strongly support the notion that distinct neural systems mediate head and body movements. Specifically, the complementary tuning between the closed-loop head and body responses suggests that their respective control is implemented differently in the brain (Fig. 2). We applied control theory to mathematically estimate the neural controllers associated with head and body control. To achieve this, we evaluated the open-loop transforms of the head and body (SI Appendix, Fig. S1). As opposed to the closed-loop transforms (Eqs. 1 and 2) that describe the relationship between the visual stimulus and motor output, the open-loop transforms describe the relationship between the measured error signal ($\epsilon$) and motor outputs ($H, B$; Fig. 3A). The open-loop transforms for the body and head are defined as:

$$G_{body} = P_{body}C_{body} \quad [4]$$

and

$$G_{head} = P_{head}C_{head} \quad [5]$$

To tease apart the plant (biomechanics) and controller (brain), we approximated parametric models of the neck and body plant mechanics. Fortunately, prior work has provided us with an idea of the general structure of these plants. Free flight and robot data have suggested that the body plant can be modeled as a first-order system mapping yaw torque to body angular velocity (14–16). We assume the same physics for our model of the body:

$$P_{body} = \frac{K_{body}}{\tau_{body} s + 1}, \quad [6]$$

where $\tau_{body}$ is the time constant, $K_{body}$ is the plant gain, and $s$ is the complex frequency from the Laplace transform. Our recent work showed that the neck mechanics of flies are elastic and overdamped, which can likewise be approximated as a first-order system (17). Using similar methods as described for the closed-loop system, we found that the open-loop body transform was best represented by a first-order model, corresponding to the plant mechanics, with a constant term in the numerator, corresponding to the controller (Fig. 3B):

$$G_{body} = \frac{e^{-0.02s}}{0.155s + 1} \ast \frac{2.23}{C_{body}} \quad [7]$$

The time delay term was necessary to model the inherent neural delay in the response. Reassuringly, the best-fit time delay (20 ms) and time constant ($\tau_{body} = 155$ ms) of the extracted body plant were consistent with previously estimated values (14, 18). Furthermore, the extracted body controller ($C_{body}$) was a proportional, or velocity sensitive, controller. This result is consistent with decades of work showing that wing steering responses in flies are strongly mediated by the rate of optic flow across the retina (19). The open-loop head transform was also fit with a first-order model, corresponding to the plant mechanics, however, an additional zero ($s$ term) in the numerator was required to fully capture the response dynamics (Fig. 3B) (see Materials and Methods):

$$G_{head} = \frac{e^{-0.02s}}{0.063s + 1} \ast \frac{0.037s}{C_{head}} \quad [8]$$

The head and body models converged to the same time delay (20 ms), but had distinct dynamics. Notably, the time constant of the head mechanics ($\tau_{head} = 63$ ms) was more than twice as fast as the body mechanics. This can be illustrated by comparing the FRFs of the parametric plant models, where we can see a clear difference in the cutoff frequencies of the head and body (Fig. 3C). Interestingly, the extracted head controller ($C_{head}$) did not consist of a proportional controller, like the body. Instead, the $s$ term in the numerator corresponds to a derivative controller (acceleration sensitive). Our conclusions were not sensitive to the choice of controller models (Fig. 3B, see Materials and Methods).

The extracted controllers of the head and body ($C_{head}$ and $C_{body}$) displayed distinct tuning to visual stimuli: proportional control for the body and derivative control for the head. To illustrate this point, we compared the FRFs of the controllers (Fig. 3D). The proportional body controller ($C_{body}$) only scaled the gain of the body plant ($P_{body}$) and had no effect on phase, however the derivative head controller ($C_{head}$) added additional gain at high frequencies and added a 90° phase lead to the head plant ($P_{head}$) (Fig. 3D). These models propose a mechanism in which body control is gated by velocity sensitive visual interneurons, but head movements act primarily on information that has gone through differentiation (i.e., acceleration) (Fig. 3E).

**A Model Derived from Flies Recapitulates Classic Primate Head-Eye Coordination Responses.** We discovered that flies implement a proportional-derivative (PD) controller but, unlike classical engineering control systems, relay the proportional and
derivative signals in parallel to two distinct motor outputs (Fig. 4A). Notably, the proportional control signal is relayed to the slower (high-inertia) motor system, whereas the derivative control signal is relayed to the faster (low-inertia) motor system (Fig. 4A). Together, these motor outputs combine for a broadband response (Fig. 4A). We call this control strategy multibody parallel proportional-derivative control (MPPD). To our knowledge, the MPPD strategy of combining actuators with distinct mechanics with a separate proportional and derivative controller has no analog in current engineering systems—however, some systems may achieve similar actuator outputs with other control strategies.

To compare gaze control in flies to other animals, we simulated the response of the head and body to a step velocity input using our closed-loop model of gaze stabilization (see Materials and Methods). The head responded quickly but also died out quickly, and the body responded more slowly, but maintained its velocity thereafter—typical of a high- and low-pass filter, respectively (Fig. 4B). A comparable experiment in primate vision showed that eye movements display a remarkably similar trajectory to head movements in flies, while primate head movements closely mirror fly body movements (Fig. 4B) (20). Although the primate visuomotor task was object tracking (position sensitive system) and the fly visuomotor task was gaze stabilization (velocity sensitive), the similar responses suggest an analogous control policy (parallel P and D control) may underlie both primate and insect active vision. Thus, MPPD may be a conserved gaze control strategy across phyla.

**An Energetic Basis for Parallel Tuning of Head and Body Control.** Why implement MPPD when using conventional PD control with one motor output might be sufficient? For example, why would flies not just control gaze just using their body? To address this question, we considered the relative mechanical energy associated with driving head and body movements. Indeed, the head and body have distinct mechanics (P_\text{head} and \( P_\text{body} \)) which require different levels of mechanical effort, or power, to move from rest. Although both the head and body mechanics are low-pass filters, the larger time constant of the body (\( \tau_\text{body} > \tau_\text{head} \)) implies that it requires more torque to move the body, especially at high frequencies. To quantify the difference in mechanical energy required to move the head and body, we designed an artificial controller to shape the body response to have the same experimental closed-loop performance as the head (Fig. 5A) (see Materials and Methods). Our simulation revealed that the body would require moderately more mechanical power to move than the head at low frequencies, but nearly 150% more power at higher frequencies (Fig. 5A). While intuitive—i.e., from physics it requires more energy to rotate a large mass than a small one—to our knowledge, mechanical energy has not been quantified when...
considering both mechanical constraints and neural control of gaze in animals. However, some human-engineered systems have been designed to take advantage of a moving camera for stabilization (21), distance estimation (22, 23), or other active sensing tasks. Here, we take another step by linking mechanics to control according to the discovered MPPD strategy. Altogether, our results strongly suggest that the neural control of the head and body is finely tuned to their corresponding mechanics, which in turn can significantly minimize mechanical energy expenditure.

The strategy of splitting control effort between active vision mechanisms to minimize mechanical energy may apply for many visually active animals. Indeed, many animals have a mobile eye(s), head or body that they move during gaze coordination tasks (SI Appendix, Table S2) (1). Insects (13), crustaceans (25), reptiles (26), amphibians (27), birds (28), mammals (29) and many other animals (2) all display similar movements of the eyes, head, and/or body. To examine how the distinct mechanics of these motor systems affect mechanical energy expenditure, we simulated the potential power savings across a broad range of motor vision systems (assuming geometric scaling and homogeneous material composition; see Materials and Methods). Our model considered the size ratio, which is defined as the ratio of the length scale of the head to the eye (e.g., primate) or the body to the head (e.g., insect) (Fig. 5B). We computed a critical size ratio of three, where 99% of the energetic benefits would be present at high frequencies ($f_c$ in Fig. 5B). Our simulation showed that all species considered had size ratios greater than three—the critical point—leading to maximum energetic benefits (Fig. 5B). At this critical size ratio of three and above, most energetic benefits are present across visual motion frequencies. Therefore, size ratio could have acted as an important evolutionary constraint on morphology in visually active animals.

**Discussion**

To achieve robust performance when tracking or stabilizing visual features moving at high speeds, animals concomitantly shift their gaze rapidly to avoid motion blur (1). Due to Newton’s laws (inertia), however, the mechanics of animals have inherently low-pass filtering properties, meaning that high-frequency movements require more mechanical power to execute. This would be especially critical for animals that engage in high-speed visuomotor tasks, such as aerial predators. While it is challenging to assess optimality in biology, the strategy we discovered exhibits two hallmarks of optimality: an overall increase in task performance and a decrease in mechanical energy expenditure. Further, our findings can inspire the application of a similar control strategy in robots employing active vision on a moving body (30).

Based on our estimates of mechanical energy savings, our results make specific predictions regarding relative metabolic energy costs of head and body movements during gaze stabilization in flight (Fig. 5). Flapping flight at low Reynolds number is highly inefficient, as the highest cost is linked to overcoming drag in a high-viscosity regime (31). Thoracic flight muscles of insects account for more than 90% of oxygen uptake in flight, and these muscles have the highest known rate of oxygen consumption for any locomotor tissue (32). To our knowledge, the energetics costs of insect flight other than those associated with contraction of the flight muscles remain elusive. It has been proposed that these costs (e.g., to move the head) would be much smaller than those associated with flight muscles (33). Complicating this interpretation however is that thoracic steering muscles may require less energy than power muscles to turn the body, and that body rotation might require slight changes in wingbeat symmetry (34). Notwithstanding, we would expect that energetic costs of turning would be dominated by actuation of the wings rather than the head, thus supporting the benefits of head actuation for high-frequency visual inputs.

An unexpected outcome from our analysis was that the MPPD control scheme uncovered in flies could capture head-eye trajectories during gaze coordination tasks in primates (Fig. 4). Previous work showed that application of optimal feedback control theory—by balancing performance (e.g., accuracy) with motor cost—could predict head-eye trajectories in primates (35). However, this application of optimal control was designed to be updated in discrete steps, which biologically would mean that primates are constantly updating a neural control policy to minimize a cost function. Here, we show that a more parsimonious control model (MPPD) that involves no feedback control theory—a more parsimonious control model (MPPD) that involves no feedback control theory—could predict head-eye trajectories in primates (35). However, this application of optimal control was designed to be updated in discrete steps, which biologically would mean that primates are constantly updating a neural control policy to minimize a cost function. Here, we show that a more parsimonious control model (MPPD) that involves no real-time tuning of neural control is sufficient to explain these same trajectories in flies and primates (Fig. 4). MPPD could still be an “optimal” solution—in the sense that the proportional and derivative control circuit gains are tuned based
on some cost function, perhaps similar to a linear-quadratic regulator (36). Together, our results provide a low-level mechanism for gaze coordination, which is likely supported by higher level feedback control and learning. Therefore, MPPD and optimal feedback control are not mutually exclusive mechanisms.

The parallel tuning of head and body neural systems we revealed is also well supported by the neural circuitry. Indeed, head and wing motor centers in *Drosophila* are enervated by many nonoverlapping neuropils (37), and head and wing movements can be decoupled when stabilizing distinct visual inputs, thus suggesting parallel neural pathways (38). It is therefore likely that neural circuits implement proportional and derivative control to drive head and body movements (Fig. 3E). While this work focuses on how vision influences gaze stabilization, our control model does not preclude the existence of inner-loop reflexes of mechanical or vestibular origin (17, 39). Indeed, the proposed parallel P and D control architecture is likely shaped by mechanosensory-based reflexes that occur on a faster time scale than visuomotor processes. An exciting future avenue will be to reveal how multisensory integration shapes the proposed MPPD control architecture. Further, our work demonstrates the importance of examining more naturalistic, closed-loop behaviors, since the lack of sensory feedback or the omission of Newtonian mechanics in the common rigidly tethered assays could influence the interpretation of sensorimotor processes (40).

In conclusion, our results suggest that animals employ an elegant solution to solve the motor redundancy problem: low-inertia motors (e.g., eyes) are recruited for high-frequency tasks and high-inertia motors (e.g., head) are recruited for low-frequency tasks. This division of labor enables efficient and high-performance gaze control. Thus, the development of a secondary mechanism to control gaze—like a mobile head or eyes—could have had substantial evolutionary benefits for visually active animals across phyla.

**Materials and Methods**

SI Appendix reports information on animal care, flight arenas, visual stimuli, kinematic tracking, parametric and nonparametric system identification, control theoretic analysis, biological scaling for energy calculations, and exploration of nonlinearities.

**Data Availability.** Data have been deposited in Penn State ScholarSphere (https://doi.org/10.26207/73lv-f846).

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**Fig. 5.** An energetic basis for parallel tuning of head and body control. (A) The process to compare the relative mechanical energy of moving the fly body (red) the same way as the head (blue) (see Materials and Methods). For the body plant mechanics, we designed an artificial controller to match the body closed-loop response to the head closed-loop experimental response. The body requires much higher controller gains to move like the head at high frequencies, leading to an increase in mechanical energy expenditure. (B) The process in (A) applied to a range of animals with different size ratios (see Materials and Methods). An increase in size ratio yields power savings by employing the smaller, faster active vision mechanism (e.g., fly head). A critical value of $\sim 3$ indicates that nearly all the energetic benefits are present when the smaller active vision mechanism is a third the length scale of that of the larger active vision mechanism. Colored lines indicate the theoretical power savings for multiple animal species and a microrobot (24) (SI Appendix, Table S2).
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