

Passive inertial damping improves high-speed gaze stabilization in hoverflies

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SUMMARY

Gaze stabilization reflexes reduce motion blur and simplify the processing of visual information by keeping the eyes level. These reflexes typically depend on estimates of the rotational motion of the body, head, and eyes, acquired by visual or mechanosensory systems. During rapid movements, there can be insufficient time for sensory feedback systems to estimate rotational motion, requiring additional mechanisms. Solutions to this common problem are likely to be adapted to an animal's behavioral repertoire. Here, we examine gaze stabilization in three families of dipteran flies, each with distinctly different flight behaviors. Through frequency response analysis based on tethered-flight experiments, we demonstrate that fast roll oscillations of the body lead to a stable gaze in hoverflies, whereas the reflex breaks down at the same speeds in blowflies and horseflies. Surprisingly, the high-speed gaze stabilization of hoverflies does not require sensory input from the halteres, their low-latency balance organs. Instead, we show how the behavior is explained by a hybrid control system that combines a sensory-driven, active stabilization component mediated by neck muscles, and a passive component which exploits physical properties of the animal's anatomy—the mass and inertia of its head. This adaptation requires hoverflies to have specializations of the head-neck joint that can be employed during flight. Our comparative study highlights how species-specific control strategies have evolved to support different visually-guided flight behaviors.

KEYWORDS motion vision | motor control | head movements | multisensory integration | frequency analysis | biomechanics | Diptera | cross-species comparison

INTRODUCTION

Agile flight maneuvers require a keen sense of vision, but without compensatory mechanisms visual processing would be severely impaired during fast movement¹. Gaze stabilizing reflexes have evolved in many animals, which reduce motion blur and keep the eyes and visual coordinates aligned with the horizon²⁻⁴. When the eyes are fixed to the head or have a limited range of motion—as in barn owls and many flying insects—head movements play a pivotal role in stabilizing gaze. The actuation of compensatory head movements is a sophisticated calculation which must handle the different time delays of the various sensory feedback systems involved, as well as taking into account the mechanical properties of the head and the range of movements the neck muscles can actuate⁵.

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The authors declare no competing interest.

SIGNIFICANCE STATEMENT Across the animal kingdom, reflexes are found which stabilize the eyes to reduce the impact of motion blur on vision—analogueous to the image stabilization functions found in modern cameras. These reflexes can be complex, often combining predictions about planned movements with information from multiple sensory systems which continually measure self-motion and provide feedback. The processing of this information in the nervous system incurs time delays which impose limits on performance when fast stabilization is required. Hoverflies overcome the limitations of sensory-driven stabilization reflexes by exploiting the passive stability provided by the head during roll perturbations with particularly high rotational kinematics. Integrating passive and active mechanisms thus extends the useful range of vision and likely facilitates distinctive aspects of hoverfly flight.

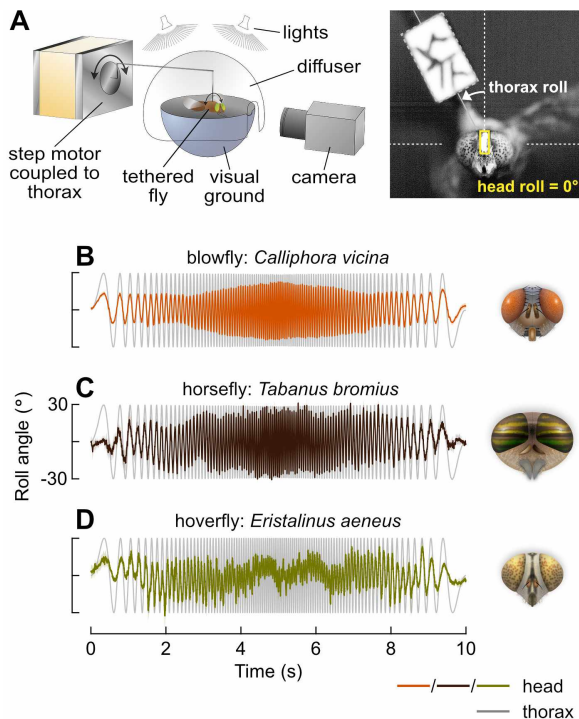


Figure 1. Hoverfly gaze stabilization performance improves at high speeds

A: Experimental setup (left). Flies were tethered at the thorax to a step motor via a piece of cardboard. Oscillations of the motor simulated thorax roll perturbations of the fly. Diffuse light was delivered from the dorsal hemisphere while a dark ground in the ventral hemisphere provided a horizon as a visual reference for stabilization. A high-speed video camera captured the resulting compensatory rotations of the head (right). Painted markers on the head and tether aided tracking.

B: Average time-series from experiments using a sinusoidal chirp stimulus, for the blowfly (*C. vicina*). The stimulus oscillated the thorax (gray trace) with a time-varying frequency profile. The absolute angle of the fly's head (color trace) is overlaid, demonstrating a stabilization effort which generally reduced the roll amplitude of the head in all species. Perfect stabilization would appear as a flat line at 0° and no stabilization effort would result in the head angle following the thorax angle, oscillating at $\pm 30^\circ$. Traces show mean head roll angle across flies. Shaded area shows mean \pm standard error (8 flies).

C: As in **A**, for the horsefly (*T. bromius*: 4 flies).

D: As in **A**, for the hoverfly (*E. aeneus*: 6 flies).

15 Sensory feedback systems with low latency are particularly
 16 valuable for stabilizing gaze during high-speed maneuvers, and
 17 in flies (Diptera) the halteres fulfill this role⁶. The halteres
 18 are a pair of club-shaped appendages on the thorax which
 19 have evolved from a rear pair of wings and act as the principal
 20 balance organs, sensing the angular velocity of the body^{7–11}.
 21 In addition, the angular position of the head relative to the body
 22 is monitored by proprioceptors, and the motion of the head is
 23 measured visually through slower processing dependent on
 24 the compound eyes^{12,13}. Many fly species also have ocelli,
 25 a set of three small, simple lens eyes on the top of the head
 26 which rapidly detect changes in orientation through differential
 27 illumination^{14,15}.

28 Since dipterans are diverse and exhibit different styles of
 29 flight and specializations of their sensory systems^{16–20}, we
 30 hypothesized that gaze stabilization would also demonstrate
 31 species-specific adaptations, whose mechanisms would reveal
 32 solutions to motor control tasks at the limits of temporal preci-
 33 sion. To test our hypothesis, we compared species from three
 34 families with contrasting behaviors: blowflies (Calliphoridae),
 35 horseflies (Tabanidae), and hoverflies (Syrphidae)¹⁶.

36 Blowflies form the basis of our comparison, since the gaze
 37 stabilization system which compensates for body-roll has been
 38 extensively studied in these species^{12,13}. Their flight is char-
 39 acterized by high-acceleration body saccades and banked
 40 turns²¹, as well as high-speed aerial pursuits launched from a

perch^{22–24} and low-speed circling around food sources prior to
 landing.

Female horseflies, on the other hand, use polarized light
 cues to detect hosts from a distance across open fields and
 exhibit direct flights toward them at speed^{25–27}. Although typi-
 cally larger than blowflies, these insects are capable of agile
 aerial maneuvers²⁸ and males are often observed hovering in
 swarms for the purposes of mating^{29–31}. The horsefly species
 we investigate here, *Tabanus bromius*, lack functional ocelli—
 the simple eyes found dorsally on the head of blowflies and
 hoverflies.

Hoverflies, while bearing similarities in many flight maneu-
 vers to blowflies, also hover with exquisite control for ex-
 tended periods, and are notable for darting and shadowing
 conspecifics, as well as their ability to fly backwards while ho-
 vering^{19,22,32,33}. We initially compared roll gaze stabilization
 performance across the three dipteran families and searched
 for differences which might reflect their flight behavior.

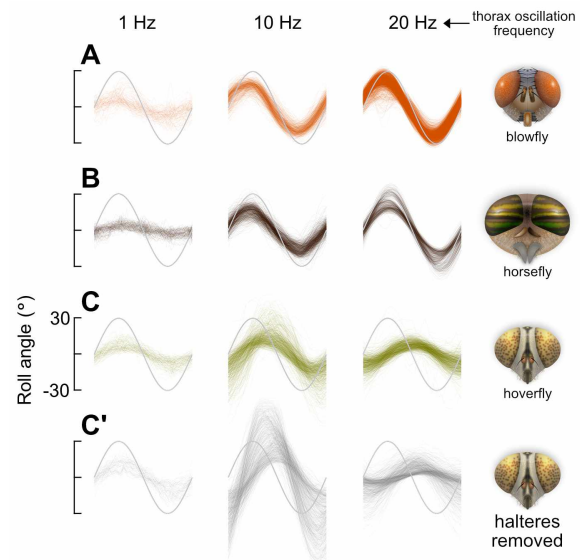
RESULTS

Hoverfly gaze stabilization improves at high speeds

To evaluate gaze stabilization performance across species, we
 used a tethered-flight paradigm and induced oscillations of the
 thorax around the longitudinal (roll) axis of the animal (Fig. 1A
 left). Experiments were captured on a high-speed camera, and
 the absolute roll angles of the head and thorax were measured

Figure 2. High-speed stabilization in hoverflies does not require haltere input

- A:** Time-series of head roll angle (color traces) in response to individual cycles of constant-frequency sinusoidal oscillations of the thorax (gray traces), for the blowfly (*C. vicina*: 5–13 flies). Perfect stabilization would appear as a flat line at 0° and no stabilization effort would result in the head angle following the thorax angle, oscillating at $\pm 30^\circ$.
- B:** As in **A**, for the horsefly (*T. bromius*: 8 flies).
- C:** As in **A**, for the hoverfly (*E. aeneus*: 6 flies). **C'**: Responses of the animals shown in **C** after removing the halteres. At 10 Hz (center), the motion of the head increased compared to the intact response, while at 1 Hz (left) and 20 Hz (right), the motion of the head was comparatively unaffected.



relative to the vertical axis in each frame (Fig. 1A right). We applied a $\pm 30^\circ$ sinusoidal chirp stimulus which varied the oscillation frequency of the thorax over time: first increasing linearly from 0 to 20 Hz in 5 s, then decreasing again from 20 to 0 Hz in 5 s. Perfect gaze stabilization would result in rotations of the head equal and opposite to those of the thorax, with zero delay, and would be reflected by a motionless head in the camera view.

At low frequencies, the gaze stabilization reflex in each species is effective at reducing the motion of the head compared to the motion of the thorax (0–1 s, Fig. 1B–D). But as frequency increases, stabilization performance decreases: the rotational speeds exceed the operating range of the sensory systems contributing to the stabilization reflex and the amplitude of head roll motion becomes progressively larger. For the blowfly, *Calliphora vicina*, head roll amplitude continued to grow until the thorax oscillations slowed down at the mid-point of the experiment (5 s, Fig. 1B, Movie 1). The same occurred for the horsefly, *Tabanus bromius*, where head roll approached the $\pm 30^\circ$ motion of the thorax, indicating an almost completely ineffectual stabilization reflex (Fig. 1C, Movie 2) (note that ‘amplitude’ refers here to the motion of the head as measured from the camera frame of reference: as stabilization performance decreases, the compensatory movements of the head relative to the thorax become smaller, resulting in increasing amplitude in the camera frame).

This negative relationship between frequency and gaze stabilization performance, above a certain frequency optimum, has previously been observed in flies^{34,35}, as well as in other animals (flying insects^{36,37}, birds³⁸, fish³⁹, reptiles and am-

phibians⁴⁰, crustaceans⁴¹, and mammals^{42,43}—including humans⁴⁴). Although it appears to be a common property across taxa—a consequence of the limited operating range of an animal’s visual and mechanosensory systems—the gaze stabilization performance of the hoverfly, *Eristalinus aeneus*, showed a different dependence on frequency. At the highest frequencies, the hoverfly’s head roll amplitude is smaller than at intermediate frequencies (Fig. 1D, Movie 3). It is also much reduced compared to the blowfly and horsefly.

To confirm that this effect was not caused by the time-varying frequency sweep contained within the chirp stimulus, we performed similar experiments using constant-frequency stimuli. Again, we observed that head roll amplitude grew larger with frequency for the blowfly and horsefly (Fig. 2A,B). For the hoverfly, head roll amplitude grew from an average of $\pm 8^\circ$ at 1 Hz to $\pm 18^\circ$ at 10 Hz—a similar increase to the other species (Fig. 2C). However, as in the chirp experiment, head roll amplitude then became smaller again at the highest speeds tested, falling to around $\pm 10^\circ$ at 20 Hz.

High-speed stabilization in hoverflies does not require haltere input

At high speeds, the predominant sensory input to gaze stabilization in the blowfly is provided by the halteres⁶. Are hoverfly halteres simply tuned to detect higher frequency oscillations than those of the blowfly and horsefly? When we repeated the previous experiment in the hoverfly *E. aeneus* after removing the halteres, head roll motion at the intermediate 10 Hz frequency was increased greatly compared to the intact response (Fig. 2C,C’ center). Indeed, head roll oscillations became larger than those of the thorax, consistent with a framework in which

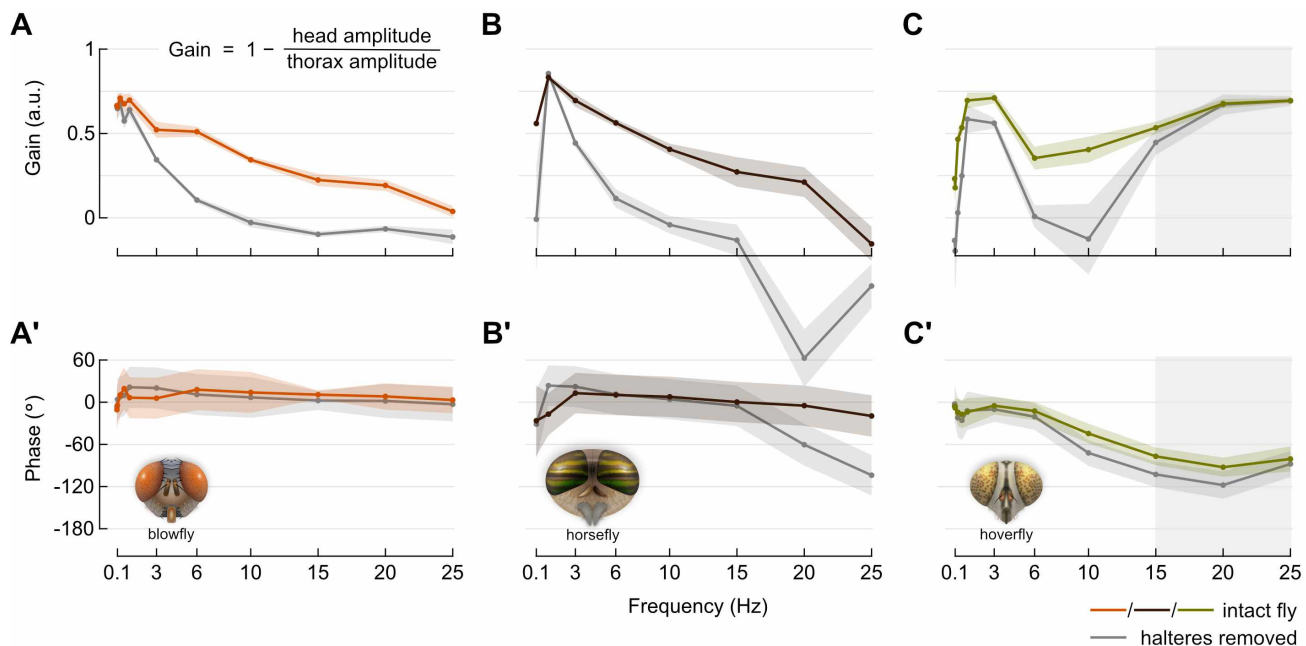


Figure 3. Gain and phase of head roll frequency-response

- A:** Average gain of the head roll response for the intact blowfly (color trace) and after removing the halteres (gray trace). Data obtained from experiments using constant-frequency sinusoidal stimuli. Shaded area shows mean \pm standard error (*C. vicina*: 5–13 flies). Head and thorax amplitudes are measured from the camera frame of reference, as in Fig. 1. **A'**: Corresponding phase angle of head roll response for the data shown in A.
- B:** As in A, for the horsefly (*T. bromius*: 8 flies). Negative gain values at 20 and 25 Hz with the halteres removed indicate increased motion of the head relative to the motion of the thorax.
- C:** As in A, for the hoverfly (*E. aeneus*: 6 flies). Gray shaded area indicates high-frequency range in which gain is unaffected by removing the halteres (gain: $P = 0.33$ at 15 Hz, $P = 0.53$ at 20 Hz, $P = 0.33$ at 25 Hz, Wilcoxon rank-sum test). **C'**: Gray shaded area indicates high-frequency range in which gain is unaffected by removing the halteres (phase: $P < 0.005$ at 15 Hz, $P = 0.041$ at 20 Hz, $P = 0.47$ at 25 Hz, Wilcoxon rank-sum test).

126 sensory input from the halteres is crucial for effective gaze
127 stabilization³⁵. Contrary to this notion, however, increasing the
128 frequency to 20 Hz with the halteres removed elicited a more
129 effective stabilization of the head: compared to the intact condi-
130 tion, haltere removal had no discernible effect on either the
131 amplitude or the phase of head roll motion at 20 Hz (Fig. 2C, C'
132 right).

133 Frequency response plots for each animal illustrate the dif-
134 ferences in their gaze stabilization behavior (Fig. 3A–C). Linear
135 gain—a proxy for performance—falls to around zero at 25 Hz
136 in the response of the intact blowfly, and at 10 Hz with its hal-
137 teres removed (Fig. 3A). For the horsefly, zero gain occurs at
138 approximately the same frequencies as for the blowfly (Fig. 3B).
139 A large negative gain is also observed at >15 Hz, which may
140 be interpreted as head roll motion being increased by the gaze
141 stabilization system at high speeds, rather than reduced: as the
142 period of the stimulus becomes shorter, the relatively constant
143 delay in visual feedback grows as a proportion of each stimulus
144 cycle duration (phase lag), ultimately causing compensatory
145 rotations of the head to be actuated at a phase which adds to
146 the thorax roll instead of reducing it.

147 For the hoverfly, gain does not fall to zero with the halteres
148 intact (Fig. 3C): the negative trend with frequency is clearly
149 reversed between 3 Hz and 6 Hz. With its halteres removed,
150 only frequencies <15 Hz are impacted: at 15, 20 and 25 Hz, we
151 found no significant difference in gain versus the intact condition
152 (Fig. 3C gray shaded area). At 0.3 Hz and below, we noted that
153 the low speed oscillations often did not elicit a large stabilization
154 effort in the hoverfly, resulting in gains well below 0.5 in both
155 conditions.

156 Two different gaze stabilization behaviors are thus evident in
157 the hoverfly frequency response: a lower-speed regime which
158 requires mechanosensory input from the halteres and a higher-
159 speed regime which operates independently of the halteres.
160 Is it possible that other sensory inputs are contributing to this
161 higher-speed regime? If the head is sufficiently stabilized, the
162 speeds of visual motion may be within the operating range of
163 the compound eyes—one of the key benefits of a stabilization
164 reflex—which would allow them to contribute to the reflex itself,
165 as they likely do at lower speeds (see gain at 1 Hz and 3 Hz
166 with halteres removed, Fig. 3C). However, the motion applied
167 to the thorax at 25 Hz exceeds 5000s^{-1} , and it is implausible

Figure 4. Slip-speed distributions demonstrate effectiveness of stabilization at different frequencies

- A:** Normalized probability distribution of visual slip experienced by the intact blowfly (color traces) during constant-frequency sinusoidal oscillations, and for the same animals after removing the halteres (gray traces). Shaded area shows mean \pm standard error (*C. vicina*: 5–13 flies). Vertical dashed line indicates theoretical maximum slip-speed experienced with no stabilization effort (i.e. head angle = thorax angle).
- B:** As in **A**, for the horsefly (*T. bromius*: 8 flies).
- C:** As in **A**, for the hoverfly (*E. aeneus*: 6 flies).

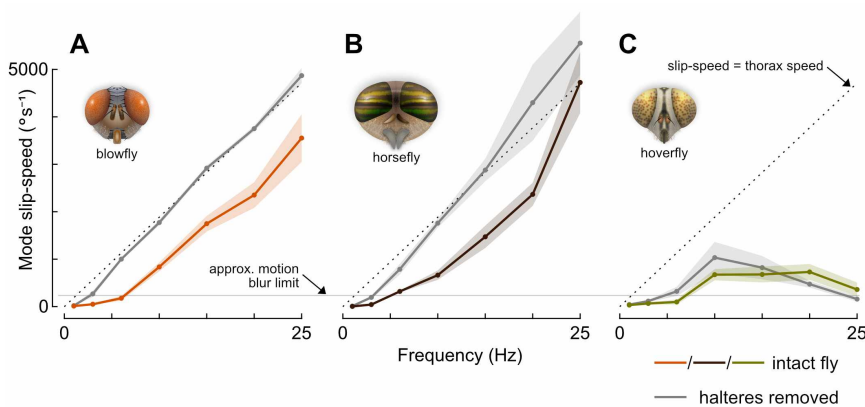
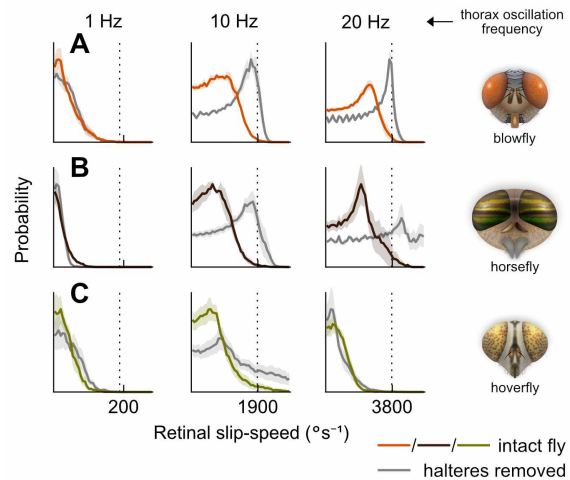


Figure 5. Gaze stabilization is effective over a wider dynamic range in hoverflies than in other flies

- A:** Mode (peak) values of the probability distributions of visual slip experienced by the intact blowfly (color trace) during constant-frequency sinusoidal oscillations, and for the same animals after removing the halteres (gray traces). Shaded area shows mean \pm standard error (*C. vicina*: 5–13 flies).
- B:** As in **A**, for the horsefly (*T. bromius*: 8 flies).
- C:** As in **A**, for the hoverfly (*E. aeneus*: 6 flies).

168 that the visual system alone is responsible for the stabilization
169 observed.

170 The phase lag (delay) calculated for the hoverfly head re-
171 sponse was considerably longer than for the other flies (Fig. 3A'
172 C', Fig. 2C). Combined with a gain close to unity, a long phase
173 lag could cause the stabilization system to increase the motion
174 of the head, rather than reduce it. We therefore asked how ef-
175 fective hoverfly gaze stabilization is at reducing head motion to
176 speeds which are within the operating range of the compound
177 eyes.

178 Gaze stabilization is effective over a wider dynamic range 179 in hoverflies than in other flies

180 At each frequency tested, we found the probability distribution
181 of retinal slip-speeds experienced by each fly, i.e. the speed of
182 visual motion across the eyes (Fig. 4A–C). For each distribution
183 we also marked the maximum slip-speed that would typically
184 be experienced if no stabilization effort were made (slip-speed
185 = thorax speed).

186 As expected for the blowfly and horsefly, the peak (mode)
187 of each distribution shifts progressively further towards higher

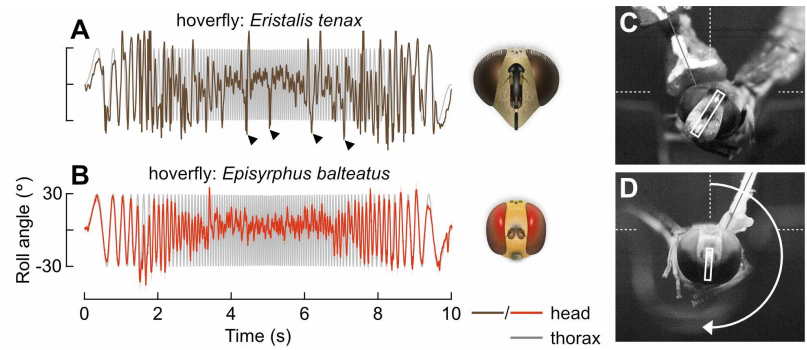
188 slip-speeds with increasing stimulus frequency, and upon re-
189 moval of the halteres (Fig. 4A,B, Fig. 5A,B). Based on typical
190 measurements of the compound eye geometry and photore-
191 ceptor response characteristics in blowflies and hoverflies, we
192 estimated the slip-speed at which motion blur would begin to
193 degrade spatial information to be between 100–200°s⁻¹ (see
194 Materials and Methods). The blowfly and horsefly both pass
195 this limit, and are far beyond it at 15 Hz, or 10 Hz with their
196 halteres removed (Fig. 5A,B), while slip-speed in the hoverfly
197 plateaus just above this approximate limit for the intact animal
198 (Fig. 5C). With the halteres removed, the mode of the slip-speed
199 distribution exceeds 1000°s⁻¹ in the hoverfly at 10 Hz, but is
200 brought under the limit at higher frequencies. We conclude
201 that gaze stabilization in *E. aeneus* is effective across a wider
202 dynamic range than in the other two species, and likely reduces
203 head motion to be within, or close to, a range in which visual
204 information is only mildly affected by motion blur.

205 Hoverfly head-neck joint facilitates stabilization through 206 inertial damping

207 We next asked whether the high-speed gaze stabilization be-
208 havior is unique to *E. aeneus*, and how it might function. To

Figure 6. Specializations of the head-neck motor system in hoverflies may enable inertial stabilization

- A:** Time-series from a single chirp experiment for a second species of hoverfly (*E. tenax*: 1 fly). Arrowheads indicate large angle, spontaneous roll rotations of the head which were uncorrelated with the stimulus.
- B:** Average time-series from chirp experiments for a third species of hoverfly. Trace shows mean head roll angle across flies. Shaded area shows mean \pm standard error (*E. balteatus*: 13 flies).
- C:** Frame capture of *E. tenax* chirp experiment during brief stabilization of the head at an offset roll angle (see [Movie 4](#)).
- D:** Frame capture of *E. balteatus* experiment showing inversion of the head (see [Movie 5](#)).



209 answer these questions we turned to two other members of
210 the Syrphidae family: the common drone fly, *Eristalis tenax*,
211 and the marmalade fly, *Episyrrhus balteatus*. In both of these
212 hoverfly species, we found stabilization behavior in response to
213 the chirp stimulus which was qualitatively similar to *Eristalinus*
214 *aeneus*, with a reduction in head roll amplitude at high frequen-
215 cies (Fig. 6A,B). This finding suggests that a similar mechanism
216 may facilitate high-speed stabilization across hoverflies.

217 During experiments with syrphids, we observed a number of
218 intriguing features of head movements that were not present in
219 the calliphorid and tabanid species we investigated—behaviors
220 which indicated specializations of the hoverfly neck motor sys-
221 tem. First, we observed an apparent loosening, or relaxation,
222 of the head-neck joint, which resulted in a distinctive ‘wobble’
223 of the head at intermediate to high frequencies (10–20 Hz).
224 Head wobble events were visible in all three hoverfly species as
225 small amplitude motion of the head (less than a few degrees)
226 at frequencies far higher than the thorax oscillation. A distin-
227 guishing feature of head wobble was periodic motion, usually
228 around the pitch or yaw axes, with a noticeable settling time
229 ([Movie 3–Movie 5](#)). These events typically occurred upon re-
230 versal of thorax motion. In each species, the head wobble gave
231 the impression of a mass rotating on a loose pivot, i.e. the
232 head-neck joint exhibited lower stiffness, damping and friction
233 than the blowfly and horsefly species, which lacked such wob-
234 ble ([Movie 1](#), [Movie 2](#)). Small mechanical juddering induced by
235 the step-motor at the extreme of each cycle appeared to shake
236 the animals, and in hoverflies the head wobbled as a result.

237 Next, we observed occasional periods of static roll angle
238 offset, during which the hoverfly’s head was stabilized and
239 relatively free of motion, but not in the default upright orien-
240 tation. Rather, the head remained rolled at an offset angle
241 (approximately 30–60°) for one or more cycles of the stimulus

([Fig. 6C](#), [Movie 3–Movie 5](#)). Erroneous sensory information
242 could explain this observation: the prosternal organs, for exam-
243 ple, detect head angle relative to the thorax and affect static
244 roll offsets in blowflies⁴⁵. However, the kinematics of the head
245 were qualitatively different to those at low frequencies (<10 Hz)
246 or in the blowfly or horsefly, and gave the impression that head
247 movements were not under active control of the neck muscles
248 during periods of offset ([Movie 3](#)).
249

250 Finally, in *E. tenax* and *E. balteatus*, large roll rotations of
251 the head occurred during experiments ([Fig. 6A](#) arrowheads).
252 In *E. balteatus*, these rotations were often extreme, completely
253 inverting the head ([Fig. 6D](#), [Movie 5](#)). The rotations occurred
254 spontaneously, in that they were seemingly uncorrelated with
255 the motion of the thorax. Notably, the head appeared to rotate
256 until reaching a mechanical limit with sufficient force that it
257 rebounded, again indicating low damping in the head-neck
258 joint. In addition, the head did not rapidly return to an upright
259 orientation upon rebound, as would be expected if the head-
260 neck joint exerted an elastic restoring force, but returned slowly,
261 wobbled, or remained at an offset, suggesting low torsional
262 stiffness ([Movie 5](#)).

263 Based on these observations, we propose that active control
264 of the neck muscle system may at times be selectively disabled,
265 allowing mechanical forces acting on the head to passively
266 influence its motion. In this state, it is possible that the inertia of
267 the head could damp forced rotations of the thorax and stabilize
268 the default orientation of the head without sensory input.

**A head-neck model captures high-speed hoverfly stabi-
269 lization behavior**
270

271 Could inertial damping explain the stabilization behavior ob-
272 served in hoverflies? Modeling a purely passive, frictionless
273 head-neck joint system with reduced torsional stiffness and
274 damping constants shows that head roll amplitude does in-

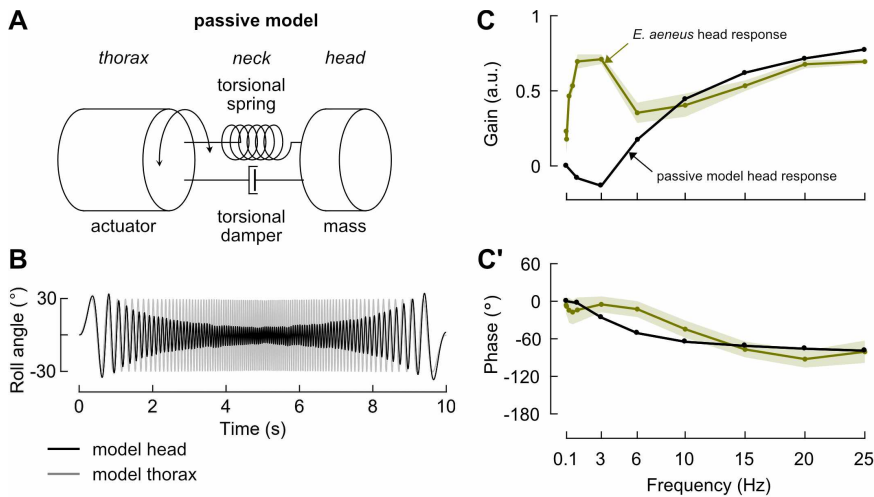


Figure 7. A head-neck model with low torsional stiffness captures high-speed hoverfly stabilization behavior

A: Diagram of a passive mechanical model of the hoverfly head, neck and thorax. The neck is modeled by a torsional spring and damper, and couples the mass of the head to the thorax, which is driven by forced oscillations.

B: Time-series from a simulated experiment using a sinusoidal chirp stimulus applied to the passive model shown in **A**. The stimulus oscillated the model thorax (gray trace) with a time-varying frequency profile. The absolute angle of the model head (black trace) is overlaid, demonstrating a completely passive, inertial stabilization which reduced the roll motion of the head relative to the thorax. Perfect stabilization would appear as a flat line at 0°.

C: Average gain of the head roll response for the model head (black trace). Data obtained from simulated experiments using constant-frequency sinusoidal stimuli. The intact hoverfly data (yellow trace) are replotted from **Fig. 3C** for comparison. **C'**: Corresponding phase angle of head roll response for the data shown in **C**.

275 deed decrease with frequency in response to a chirp stimulus
276 (**Fig. 7A,B**), strongly resembling the behavioral response ob-
277 served in hoverflies at high frequencies (**Fig. 1D**, **Fig. 6A,B**).

278 Simulations of constant-frequency oscillations further
279 demonstrate that at low frequencies—up to around 3 Hz—the
280 forces on the head are insufficient for inertial damping to sta-
281 bilize it, and the motion of the head approximately follows the
282 thorax, which results in gains close to zero (**Fig. 7C**, **Fig. S1A**).
283 For the hoverfly *E. aeneus*, gains are higher than predicted by
284 the passive model in the range 0.06–3 Hz (**Fig. 7C**), indicating
285 an active gaze stabilization reflex that depends on sensory
286 input. Where the gain of the hoverfly response drops between
287 3–10 Hz, the gain in the passive model increases as inertia
288 begins to affect head motion. Between 10–25 Hz, the gain
289 and phase of the passive modeled response closely match the
290 hoverfly data (**Fig. 7C**, **C'**), with a similar plateau in slip-speeds
291 at around 600°s^{-1} (**Fig. S1C**, **Fig. 5C**). This leads us to con-
292 clude that passive, inertial damping alone, with no sensory
293 input, could provide effective gaze stabilization at high speeds,
294 provided that the stiffness and damping of the head-neck joint
295 are appropriately low.

296 DISCUSSION

297 Here we have presented lines of evidence which support a view
298 of gaze stabilization through inertial damping in hoverflies. This
299 passive behavior enables effective stabilization of the head and
300 eyes while the thorax is free to roll at extremely high angular

301 velocities and accelerations. While we uncovered this behavior
302 in a tethered-flight paradigm with a motor actuating roll oscilla-
303 tions of the thorax, we expect that it would be similarly activated
304 in response to external disturbances in free-flight, such as wind
305 gusts.

306 The repetitive, oscillatory motion of the sinusoidal stimuli
307 used in our experiments is clearly different to that of a wind
308 gust, and investigating responses to an abrupt, step-like rotation
309 of the thorax would have been desirable in this sense. The
310 prohibitively high inertia of the motor used in our setup did not
311 allow us to generate roll accelerations well approximating a
312 step function. Goulard et al.⁴⁶, however, were able to induce
313 step-like thorax rolls in *E. balteatus*. In their study, the hoverfly
314 head showed an amount of overshoot upon step rotations which
315 is congruous with the low stiffness and damping of the neck
316 which we propose allows inertia to stabilize the head.

317 Inertial gaze stabilization in the context of hoverfly flight 318 behavior

319 Inertial gaze stabilization, which was unaffected by removing
320 the mechanosensory input from the halteres, was observed in
321 our experiments at oscillation frequencies of 15 Hz and greater.
322 At 15 Hz, the maximum angular velocity applied to the thorax
323 was around $2800^{\circ}\text{s}^{-1}$, and maximum acceleration was around
324 $2 \times 10^5 \text{s}^{-2}$. Do hoverflies actually encounter roll rotations with
325 comparable kinematics during flight? Previous studies which
326 have captured the free-flight behavior of hoverflies (*E. tenax*,
327 *E. balteatus*, and various other species) either did not resolve

or report roll rotations of the thorax^{22,47–51}, but similar experiments with blowflies (*C. vicina*) recorded roll velocities in excess of $2000^{\circ}\text{s}^{-1}$ and accelerations on the order of 10^5s^{-2} during fast U-turn maneuvers and saccades²¹. Meanwhile, landing maneuvers made by *C. vomitoria* can involve a rapid inversion of the body about the roll axis, with velocities approaching $6000^{\circ}\text{s}^{-1}$ ⁵². These volitional maneuvers took place in relatively small, confined arenas, and even higher values may well be expected in the wild.

However, our experiments captured reflexive behavior in response to roll rotations caused by an external disturbance, rather than voluntary movements. One study examining the impact of such external perturbations on insect flight demonstrated that hovering bees (*Apis mellifera*) are capable of rapid recovery from a wind gust which caused roll rotations with similar kinematics⁵³. In another study, a sudden free-fall situation was imposed on stationary hoverflies (*E. balteatus*) hanging from a ceiling, which induced a righting maneuver to recover from the tumble⁵⁴. In these experiments, extremely high roll rates of over $10 \times 10^3\text{s}^{-1}$ were recorded. The animals' ability to regain stability after such perturbations makes it reasonable to assume that they regularly encounter such excessive attitude changes during natural flight in turbulent conditions.

Why, then, does it appear that hoverflies employ inertial gaze stabilization while other highly maneuverable flies like blowflies do not? We find clues to answer this when we consider the distinguishing flight behavior of hoverflies—namely, hovering, for the purpose of visiting flowers, guarding territory and seeking mates. While hovering, flies may be particularly susceptible to being rolled by gusts of wind. Lateral instability is higher when hovering than during forward flight^{55,56} and angular velocities around the roll axis are typically higher than those around pitch or yaw for an insect flying in turbulent conditions, due to a smaller moment of inertia⁵⁷. Hoverflies also seem to be equipped for more agile flight than the other dipteran families we investigated here: wide-field motion sensitive visual neurons in hoverflies respond more rapidly than the homologous neurons in *Calliphora* spp., for example¹⁹, and are greater in number in each individual animal^{18,58}. They also maintain sensitivity across a wider range of temporal frequencies of image motion¹⁷.

Hovering in hoverflies may therefore be particularly demanding in terms of flight maneuvers and stabilization reflexes. The gaze stabilization system in other flies might not be required to operate at a dynamic input range that includes such high angular accelerations that may occur while holding a hovering

position for extended periods or during the initial phase of an aerial pursuit. Another possibility is that the visually-guided behaviors which hovering flight supports are also highly demanding in hoverflies and necessitate this alternative stabilization method. For example, the detection of conspecifics before initiating aerial pursuits from hovering likely requires near-constant high-acuity, stabilized vision, which may be a less demanding sensorimotor task for ground-launched pursuits. Likewise, the flight reflexes to recover from a gust-induced tumble may tolerate some degree of brief motion blur due to passive stability afforded by the body and wings.

Anatomical specializations of the head-neck joint

How could the head-neck joint work in hoverflies to enable inertial stabilization? First, we posit that a flexible joint is required, with lower stiffness and damping than the equivalent joint in the species of blowfly or horsefly investigated here. Low friction in the joint is also necessary, to allow the head to effectively spin freely while the thorax rotates. When allowed to spin freely, rotations of the thorax are decoupled from the head. The head then tends to remain in a default orientation as a result of its inertia—at least, for a certain range of rotational accelerations.

Below this range, the effect of inertia is insufficient to overcome the torsional stiffness of the joint. The head is then more strongly influenced by rotations of the thorax and inertia provides little stabilization, as seen in the response of a purely passive model of the head-neck system at low frequencies (Fig. 7B). It is within this range that active, sensory-driven stabilization is required, which we discuss further in the next section.

Some of our observations highlight that there may be consequences of a flexible head-neck joint and inertial stabilization which are not obviously beneficial. At times, the head became stabilized at an offset from the default level orientation (Fig. 6D), with the constant error of the head angle going uncorrected over multiple stimulus cycles. A similar uncorrected head angle error was reported in a previous study, apparently as result of overshoot from a step rotation⁴⁶. We suggest that the overshoot itself may have been caused by the freely spinning head-neck joint. Even without sensory input and stabilizing reflexes, these events would not be expected to occur in other species, where elasticity in the neck motor system likely provides a passive restoring force to correct for static offsets during flight⁵⁹.

The second requirement for the hoverfly head-neck joint is an ability to switch between the aforementioned passive, free-spinning mode and a mode in which the muscles of the neck motor system exert control over the movement of the head.

Active head movements are made during flight, not just around the roll axis, but also around pitch and yaw^{5,47}. Grooming, feeding and other behaviors also require fine motor control of the head. A mechanism should therefore exist to temporarily disengage the neck motor system. Its point of action could be the physiology of the muscles or their mechanical coupling of the head and thorax—a feature which could be resolved with fast in vivo imaging⁶⁰.

Surprisingly, both of these requirements appear to be met by properties of the head-neck joint in another flying—and hovering—group of insects: the dragonflies and damselflies. The ‘head-arrester’ system found in the adults of all known species of Odonata is an arrangement of muscles and skeletal structures in the neck joint which mechanically lock the head to the thorax^{61,62}. Movement of the head can be selectively enabled by release from the arrested state. The head pivots at a single-point and folds in the connective membranes of the arrester system impart a high degree of flexibility to the joint⁶³. The main purpose of the head-arrester system is thought to be reinforcement of the neck, which is generally very thin compared to the size of the head and a mechanical weak-point^{62,64}. During certain behaviors, such as feeding or tandem flights, the head is arrested in order to prevent injury to the neck^{61,65}.

For agile flight maneuvers, such as chasing, the dragonfly head appears to be free to move and, just as in the hoverfly, inertia acts to stabilize it in a default orientation⁶¹. A passive gaze stabilization system may be advantageous in dragonflies and damselflies, since they lack the specialized fast mechanosensory input provided by the halteres in Diptera. The head is also typically larger and of greater mass in dragonflies than in hoverflies, which may help to passively maintain a default orientation of the head even without dynamic movement⁶¹. Intriguingly, in the un-arrested state certain contact points between structures in the head-neck joint become physically separated, causing fields of mechanosensory sensilla on their surfaces to be disabled⁶². These sensilla usually monitor the position of the head relative to the thorax and appear to be involved in flight reflexes and gaze stabilization^{61,62}. Without this proprioceptive information, offsets in the roll angle of the head can go uncorrected during inertial stabilization in dragonflies, just as we and others⁴⁶ have observed in hoverflies.

The anatomy of the neck-motor system is well-described in dragonflies and blowflies, and they exhibit many fundamental differences to each other^{5,61}—unsurprising, given their evolutionary divergence². Similar descriptions are unfortunately lacking in hoverflies, and we can only speculate as to how iner-

tial stabilization of the hoverfly head may be selectively enabled and disabled. However work is now underway to provide a detailed anatomical study and to search for a mechanism which may be functionally equivalent to the odonate head-arrester system.

A hybrid gaze stabilization system with active and passive components

Hoverflies show a remarkably improved gaze stabilization performance at high stimulation frequencies, presumably enabled by a passive, inertial mechanism. An inertia-driven system appears only to operate under high rotational accelerations in hoverflies. At stimulation frequencies below 15 Hz, we observed a gaze stabilization reflex which largely resembles those found in the blowfly and horsefly, whereby sensory input is required. In this lower dynamic range, the halteres play a significant role by sending a forward signal to initiate fast compensatory head movements with low response latency. This reduces the motion of the head—and thus the retinal slip speed—sufficiently to allow the motion vision pathway to also provide feedback signals to the stabilization reflex^{35,66}.

All three families share this general principle of sensory-driven, active stabilization, while hoverflies also exhibit a family-specific adaptation to cope with a higher dynamic range. Without the response latency incurred by sensory transduction, neural processing, and the actuation of muscles in the neck-motor system, an inertial system provides clear benefits during flight maneuvers with particularly high accelerations, such as hovering or departures from hovering. As with the control of flight, passive stability can counterbalance the loss of fast sensory input⁶⁷. And similar to damselflies and dragonflies, the hybrid system that hoverflies have developed is a prime example of morphological computation^{68,69} where functional anatomical structures enable the highly effective performance of specific sensorimotor control tasks. The design of energy-efficient, artificial image stabilization systems may take inspiration from this novel biological approach⁷⁰.

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DATA AVAILABILITY The data and analysis code generated during this study are available at the Open Science Framework: <https://osf.io/bhytv>

AUTHOR CONTRIBUTIONS Ordered according to main list of authors:

Conceptualization: BJH, HGK
Data curation, validation: BJH
Formal analysis: BJH, FJHH, DAS
Funding acquisition, resources, administration: HGK
Investigation: BJH, KB
Methodology: BJH, KDL, DAS
Software: BJH, FJHH, KDL, DAS

521 **Supervision:** KDL, HGK

522 **Visualization:** BJH, FJHH

523 **Writing – original draft:** BJH, HGK

524 **Writing – review & editing:** BJH, KB, FJHH, KDL, DAS, HGK

525 MATERIALS AND METHODS

526 **Animal collection and preparation** Wild-type, adult female
527 flies of indeterminate age were used for all experiments.
528 Blowflies, *Calliphora vicina*, were collected from a colony raised
529 in lab conditions at 20°C, on a 12:12 hour dark:light cycle. Wild
530 horseflies, *Tabanus bromius*, were caught in fields in Buck-
531 inghamshire, UK and near Ljubljana, Slovenia. Wild hover-
532 flies, *Episyrphus balteatus* and *Eristalis tenax*, were caught in
533 Buckinghamshire, UK. Hoverflies raised in commercial colonies
534 were also used, transported as pupae: *Eristalinus aeneus*
535 from Bioflytech SL, Spain, and *Episyrphus balteatus* from Katz
536 Biotech AG, Germany. Prior to experiments, animals were
537 kept in net cages with conspecifics. Individual flies were col-
538 lected from their cage and cooled on ice in a vial. A cardboard
539 tether was attached to the pro-thorax using beeswax. The
540 tether was oriented to give an approximately 0° attitude of the
541 body during tethered-flight. For experiments with the halteres
542 removed, the shaft of the halteres was severed as close as pos-
543 sible to its base using sharp micro-dissection scissors. Normal
544 wing-stroke, leg-tuck and head movements were verified before
545 experiments. Although we considered testing anesthetized or
546 sacrificed animals, finding a lack of inertial stabilization in this
547 condition could have a number of possible causes, such as a
548 disabled mechanism for switching to a passive head-neck joint.

549 **Experimental setup** Tethered animals were secured to a step-
550 motor which was controlled by a micro-stepping driver (P808,
551 Astrosyn). The motor step resolution used was either 5000 or
552 3200 steps per revolution, for 0–10 Hz or 15–25 Hz oscillations,
553 respectively. The motor driver was controlled through Matlab
554 (R2014a, Mathworks) via a DAQ (NI-6025E, National Instru-
555 ments). A hemispherical false horizon made of black-painted
556 plastic, approximately 50 mm diameter, was positioned beneath
557 the animal with the top edge close to the eye equator. A slightly
558 larger diameter translucent white plastic hemisphere was posi-
559 tioned above the fly to form a light diffuser which encompassed
560 the horizon (Fig. 1A). Illumination was provided by four light
561 guides (KL 1500, Schott). Luminance at the position of the
562 animal was measured to be 500 Cd m⁻². A small opening in
563 the front of the horizon permitted a head-on view of the ani-
564 mal. Airflow was applied continuously during experiments to
565 encourage flight.

Two high-speed cameras were used to record experiments:
one for shorter experiments (Fastcam SA3, Photron) with a
100 mm macro lens (Zeiss), and one with higher storage ca-
pacity for longer experiments (Phantom v211, Vision Research)
with a 180 mm macro lens (Sigma). Aperture sizes were ad-
justed between $f/3.5$ – 5.6 depending on the length of the animal
and depth-of-field required. Frame-rates up to 1200 fps were
chosen according to the length of the experiment and the stim-
ulus frequency, ensuring at least 1 frame per 2° of rotation.

Stimulus protocol The chirp stimulus time-series was defined
as:

$$x(t) = A \sin(2\pi f_0 t + \pi r t^2),$$

where A is the oscillation amplitude (30°), f_0 is the initial fre-
quency (0 Hz), t is the time vector, and r is the chirp rate—the
rate of change in frequency—over the time interval, T (10 s):

$$r = (f_{max} - f_0) / T$$

A positive and a negative chirp rate were used within each
experiment:

$$r(t) = \begin{cases} +4, & \text{for } t \leq 5 \text{ s} \\ -4, & \text{for } t > 5 \text{ s} \end{cases}$$

with a maximum frequency, f_{max} , of 20 Hz. Experiments us-
ing constant-frequency stimuli varied in length and number of
cycles, from 3 cycles at 0.06 Hz to 250 cycles at 25 Hz. Ex-
periments using 15–25 Hz stimuli required an initial ramp in
amplitude to overcome the inertia of the step motor: the ampli-
tude reached $\pm 30^\circ$ within 2 s, and 10 s of subsequent cycles
were analyzed per experiment.

Video analysis Recorded experiments were analyzed auto-
matically to extract the roll angles of the head and the card-
board tether in each video frame. Analysis was carried out in
Labview (v2013, National Instruments) using a modified version
of a previously-developed custom template-matching method⁷¹.
Only experiments in which the animal flew continuously for all
stimulus cycles were analyzed. Subsequent analysis of roll an-
gle time-series was carried out in Matlab (2020b, Mathworks).

Maximum stimulus velocity For constant-frequency sinu-
soidal oscillations, the angular velocity of the stimulus var-
ied throughout each cycle. For plots of slip-speed distribution
(Fig. 4, Fig. S1) we marked the theoretical maximum slip-speed
experienced with no stabilization effort (i.e. head angle = thorax
angle), which we calculated as the maximum angular velocity
of the stimulus in each cycle:

$$2\pi f A,$$

608 where f is the oscillation frequency and A is the oscillation
609 amplitude.

610 **Motion blur limit** The retinal slip speed at which motion blur
611 occurs was approximated from a rule-of-thumb of one photore-
612 ceptor acceptance angle per response time⁷². With an esti-
613 mated range of acceptance angles of 1–2° for the species stud-
614 ied^{73,74} and a response time of 10 ms, motion blur would be
615 expected to begin to degrade visual information at slip speeds
616 around 100–200°s⁻¹ and higher. Note that this does not imply
617 an upper limit to useful motion vision—responses in motion-
618 sensitive neurons in Diptera have been recorded at greater
619 image velocities¹⁷.

620 **Head-neck model** A previously-developed model of the dy-
621 namics of blowfly gaze stabilization⁷⁵ was modified to include
622 only the passive physical properties of the head and neck. The
623 following equation of motion for the head was solved at discrete
624 time intervals:

$$625 \quad J\ddot{\theta}(t) + c\dot{\theta}(t) + k\theta(t) = c\dot{\phi}(t) + k\phi(t),$$

626 where θ is the roll angle of the head, ϕ is the roll angle of the
627 thorax (determined by the chirp stimulus time-series described
628 above), k and c are the torsional spring and damping constants
629 of the head-neck joint, respectively, and J is the moment of
630 inertia of the head, defined for a thin-walled spherical shell
631 (approximating the hoverfly head) as:

$$632 \quad J = \frac{2}{3}mr^2,$$

633 where m is the mass of the sphere and r is its radius.

634 The following values for physical parameters were used:
635 $m = 10 \times 10^{-6}$ kg, $r = 0.002$ m, $J = 2.66 \times 10^{-11}$ kg m²,
636 $k = 1 \times 10^{-8}$ N m deg⁻¹, $c = 1 \times 10^{-9}$ N m s deg⁻¹. The values
637 chosen for k and c were one order of magnitude smaller than
638 those estimated for the blowfly⁷⁵, in order to investigate the
639 proposed low stiffness and damping of the hoverfly head-neck
640 joint.

SUPPLEMENTARY INFORMATION

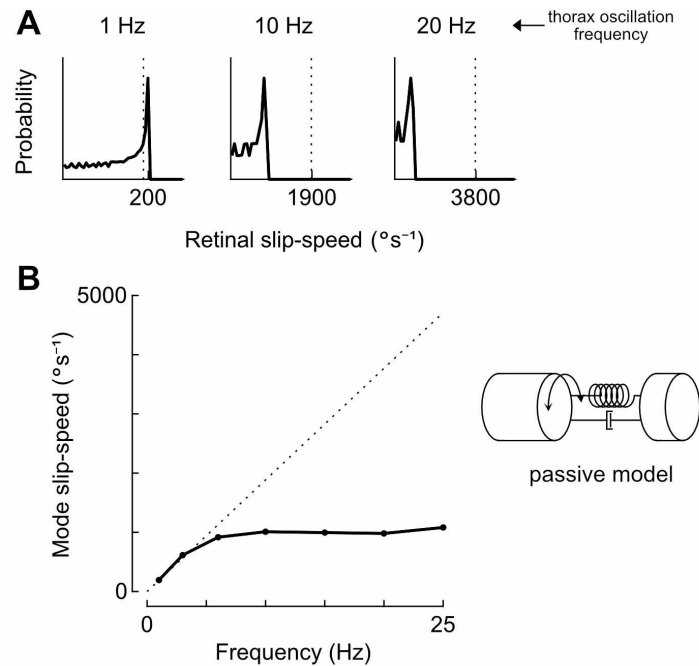


Figure S1. Slip-speed distribution at different frequencies for the head-neck model

A: Normalized probability distribution of visual slip experienced by the passive model head shown in Fig. 7, during simulated constant-frequency sinusoidal oscillations. Vertical dashed line indicates theoretical maximum slip-speed experienced with no stabilization effort (i.e. head angle = thorax angle).

B: Mode (peak) values of the probability distributions of visual slip experienced by the passive model head during simulated constant-frequency sinusoidal oscillations.

Movie 1. High-speed video of *C. vicina* chirp experiment <https://osf.io/qyc3m>

Movie 2. High-speed video of *T. bromius* chirp experiment <https://osf.io/sntdf>

Movie 3. High-speed video of *E. aeneus* chirp experiment <https://osf.io/d3njt>

Movie 4. High-speed video of *E. balteatus* chirp experiment <https://osf.io/4zrpa>

Movie 5. High-speed video of *E. tenax* chirp experiment <https://osf.io/s6kj3>