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14. ABSTRACT: Our results show that the fly gaze stabilisation reflex in general has the properties of a low-pass filter - the shape of the gain and phase plots illustrate this perfectly. However, as our later experiments involving the halteres show, two parameters of the filter - corner frequency, cut-off - are not defined by the motor system, but change according to the available sensory information. Low-frequency performance is maintained through sensory input from the compound eyes, while the addition of sensory input from the halteres smoothly extends the range of the reflex to much higher frequencies. Interestingly, sensory input from the ocelli gives a small advantage across the entire frequency range whereas, given the phasic nature of ocellar inputs to VS neurons, we would have expected little or no difference at frequencies where the period of the waveform approaches _500ms (Simmons et al., 1994). In general however, the size of the reduction in latency of the headroll reflex with ocellar input matches what we would expect from our previous electrophysiology experiments (Parsons et al., 2006, 2010). Our data perfectly complement those of Hengstenberg, Hengstenberg & Schuppe (Hengstenberg, 1993; Schuppe & Hengstenberg, 1993). In these earlier studies, the authors characterised the headroll reflex in terms of sensitivity at different angular velocities of motion. Here we have described the reflex in terms of frequency response - these data are essential so that we can begin to model the fly's control system with a firm grasp of the real physical parameters. Now we have a more complete picture of the filtering properties of the entire reflex, as well as the individual sensors - the compound eyes, ocelli and halteres - the next step in this process will involve measuring some of the physical properties of the motor system, while further probing the integration of sensory signals at the motor neuron level. While continuing to expand our description of the headroll reflex, we also intend to extend our study to the fly's body stabilisation reflex. The dynamics of whole-body stabilisation are completely different to those of head stabilisation, so we would expect this to be reflected in the frequency response of the flight stabilisation reflex.

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Sensor Fusion for Feedback Control of Gaze Stabilisation in the Fly

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Contents

1 Summary

Multisensory integration, or sensor fusion, is currently of fundamental interest to the scientific community in general (Stein & Stanford, 2008; Nassi & Callaway, 2009). Research in this area increases our understanding of more central areas of the brain, where sensory information converges. It will guide further quantitative studies of the nervous system in these areas, and helps to form a more complete picture of the processing that drives sensory-guided behaviour. It is also expected, and desired, that this type of work may provide inspiration for applications - in our particular case - for the design of compact, efficient and robust MAV flight control systems. We have chosen gaze stabilisation as our experimental paradigm because it is a robust and ubiquitous reflex, present in many different forms across phyla. It is also highly scientifically tractable: here we confined our study to a single degree of freedom (roll rotation) thus simplifying both experimental protocols and analyis, but we are still able to assess the overall performance of the system. Here we provide a frequency-domain and step-response analysis of the fly headroll reflex, with a focus on the performance of the two visual systems. We also report the frequency response of the reflex with additional stimulation of the the fly's fast mechanosensory system, the halteres. These data reveal the extent to which the dynamic range of the reflex is altered as the ocelli and/or the halteres are disabled, and enhance our overall description of the fly's stabilisation system.

2 Introduction

Rapid and effective flight control is critically important for the blowfly. Its aerodynamic instability permits outstanding manoeuvrability but increases the demands placed on flight control. To achieve speed and accuracy, the fly's nervous system integrates input from several sensors, as revealed by intensive studies of the fly's ability to compensate for rotational deviations, or changes in attitude, during flight (Hengstenberg, 1993). A recent review has related the way in which an insect's flight control system gathers and processes information to the demands made by its aerodynamics (Taylor & Krapp, 2007). One of the key hypotheses generated by this comparison is that information is being collected by sensors and processed by neurons in coordinates that are closely related to the axes of flight instability. This correspondence brings two advantages; it applies the limited information capacity of the nervous system to the most important regions of input space and it generates output vectors whose axes are most effective for control. The review also emphasises the importance of gathering information from sensors with different dynamics. It is particularly noteworthy that three sensors cover overlapping sections of the time domain. For instance, following the sudden initiation of a rapid roll the inertial sensors of the halteres respond within 5 ms, the optically driven ocelli kick in at $\approx$10ms, while the motion sensors of the compound eye take of the order of 20 ms to register a change.

The behavioural work described in this report follows on from our comprehensive description of the responses of VS neurons in the lobula plate to rotational stimuli applied to the ocelli. This fusion of information from the ocelli and the compound eyes is described in the previous report and has since been published (Parsons *et al.*, 2010). We have now completed behavioural experiments which describe the closed-loop frequency response of the fly's gaze stabilisation reflex. Using two different stimulus protocols, we were able to assess the contributions that each of the flies 3 main sensory systems: the compound eyes, the ocelli and the halteres, make to a basic stabilisation reflex. Our new data confirm that, as predicted by the electrophysiological data from VS neurons, the ocelli contribute to stabilisation and reduce response latency. Our data also suggest that the halteres play the major role in generating high gain, low latency responses to high-frequency, periodic perturbations.

3 Methods

Most of the results in this report are derived from high-speed video footage of the head movements of tethered flying blowflies, *Calliphora vicina*. Both the description of the stimulus apparatus for generating apparent roll by rotating the visual surroundings, and the method used for automated extraction of the head angle, can be found in our previous progress report (Parsons *et al.*, 2009).

3.1 Frequency-domain analysis of high-speed video data

In general, the most direct route to obtaining the frequency response of a control loop is to input some type of broadband signal, and then extract the frequency components using Fourier techniques. However, this requires one to spread the signal power equally, or at least according to some function, across the frequency range. This is often only appropriate - even if the system is linear - if there is either i) very little noise in the system, or ii) large, or unlimited recording time. In many animal behaviour experiments, including the ones described in this report, neither of these conditions are met, and some degree of nonlinearity is to be expected, so a more robust method is necessary, i.e. driving the system with single-frequency sinusoids. This gives a large signal-to-noise ratio in the behavioural output, and allows for a relatively low-error estimate of the response at that frequency.

We recorded head movements during stimulation with sinusoidally oscillating roll at a range of frequencies from 0.4 - 25Hz. Raw video data were then converted into records of head position and stimulus position as described in (Parsons *et al.*, 2009). A nonlinear least-squares sinusoid fitting algorithm (Matlab ® Curve Fitting Toolbox) was first applied to the stimulus data, to obtain the precise frequency f_S, amplitude A_S and phase ϕ_S of each applied waveform, thus allowing for any errors generated in the step motor used to deliver the stimuli. The parameters of the stimulus fit were used as a starting point for the algorithm, now applied to the response (head position) data. The response fit was constrained such that $f_R = f_S$ and $\phi_R \leq \phi_S$, to obtain the response only at the stimulus frequency, and ensure a phase lag of the response behind the stimulus, not a phase lead.

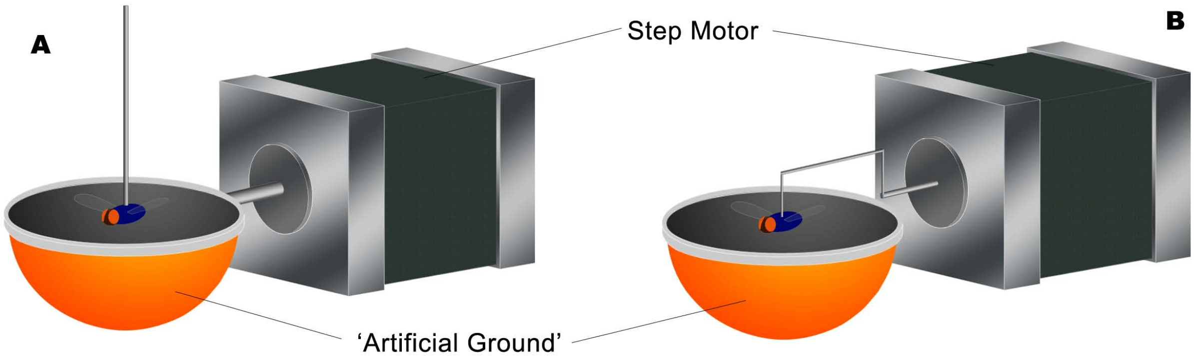

Figure 1: Apparatus for stimulation of mechanosensory (halteres) and visual (compound eyes, ocelli) sensory systems. The visual systems are isolated using the ego-static stimulus paradigm (**A**), while all systems are engaged with the ego-motive paradigm (**B**).

The latency of the response was calculated with two different methods, both of which gave similar results. Firstly, the phase difference calculated using the method above was converted to a latency according to the measured stimulus frequency and the frame rate of the video camera (250fps). Secondly, the latency was obtained by temporal cross-correlation of the fit to the stimulus with the fit to the response.
All the error bars displayed in this report mark the standard error on the mean (SEM) of values pooled from four flies, and as such primarily indicate inter-individual variability. The confidence intervals for the sinusoidal fits to individual frequency response data were generally smaller than the SEM across a set of individuals.

3.2 Analysis of step response data

Step changes in stimulus angular position were applied with a range of constant-gradient ramps with amplitudes of 30° or 60°. To measure the latency of the resulting compensatory head movement we estimated, by hand, the time of initiation of the response - this was defined as the approximate position of the 'corner' of the response ('corner' of the stimulus being the beginning of the step). Hand measurement was appropriate in this case because it was the fastest method for obtaining a reliable estimate, and temporal cross-correlation was found to be unreliable for single step stimulus/response pairs. We attached a generous error margin of ±4° to this measurement. For Figure 7, the final position of the stimulus or the head between ramps was defined as the mean of the central 50% of data points between the end of one step and the onset of the next.

3.3 Mechanosensory stimulation

Our experiments up to this point were concerned with assessing the contributions of the fly's two visual systems, using ego-static stimulation, i.e. the fly is tethered in a fixed position, and the stimulus hemisphere is rotated with a step motor (Fig. 1A). To extend our study, we added an ego-motive stimulus protocol (Fig. 1B) where the stimulus hemisphere is fixed, and the fly is tethered directly to the step motor. This engages the animal's mechanosensory systems, in addition to stimulating the visual systems as before. Experiments were carried out with this protocol as described earlier, and the resulting data processed in a similar way.

4 Results and Discussion

4.1 Frequency response of visually-mediated headroll reflex

We applied visual sinusoidal rotation stimuli (see Methods) to tethered, flying flies, at discrete frequencies ranging from 0.4 to 25hz, with an amplitude of 30° (60° peak-to-peak). The resulting head

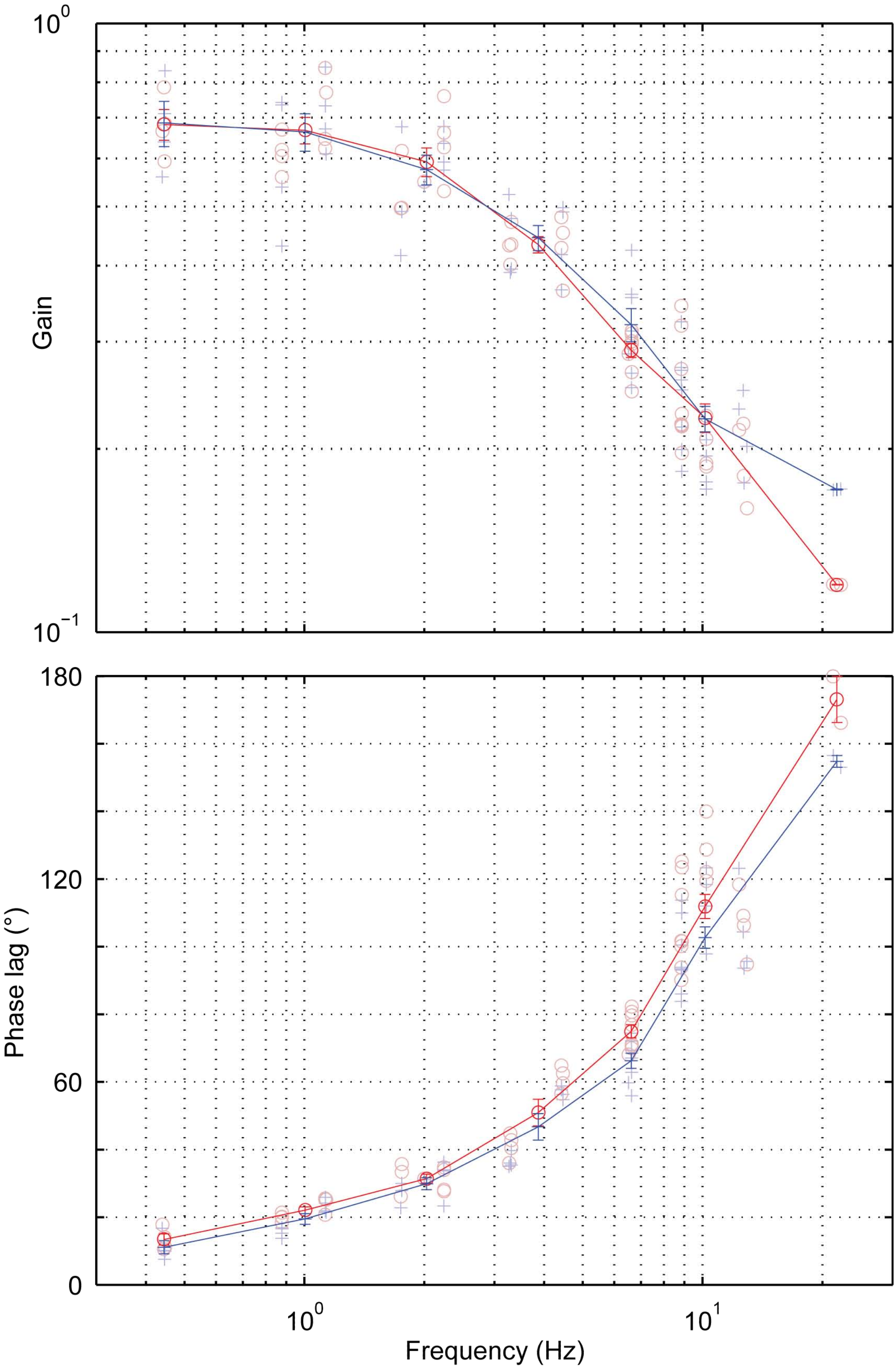

Figure 2: Bode plot of visually-mediated compensatory headroll movements across a frequency range of approximately 0.4 - 25 Hz (4 flies, n = 70). The faded symbols mark the mean measurements at single frequencies from individual flies, while the solid line and bold symbols mark the mean of measurements from all flies. The blue crosses mark data obtained while both visual system were operational, while the red circles mark data obtained after occlusion of the ocellar lenses.

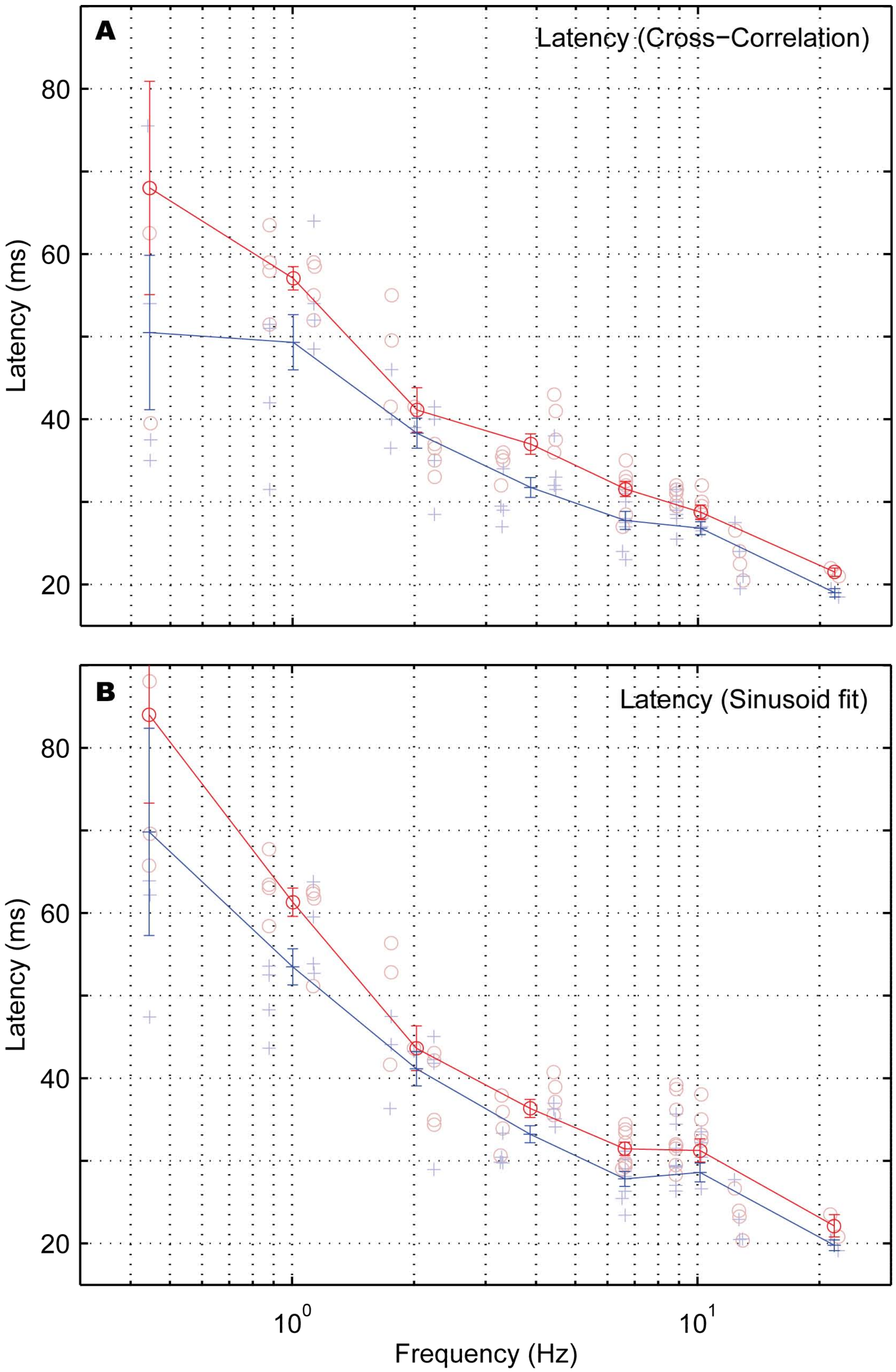

Figure 3: Response latency of visually-mediated compensatory headroll movements across a frequency range of approximately 0.4 - 25Hz (4 flies, n = 70). Latencies were calculated via two methods: temporal cross-cross correlation (**A**) and phase difference (**B**) of stimulus and response waveforms (see Methods). The faded symbols mark the mean measurements at single frequencies from individual flies, while the solid line and bold symbols mark the mean of measurements from all flies. The blue crosses mark data obtained while both visual system were operational, while the red circles mark data obtained after occlusion of the ocellar lenses.

movements were captured with a high-speed video camera (Photron FastCam SA3) at 250fps. The video data were then converted, via a semi-automated image processing algorithm (constructed in National Instruments Labview + Vision) into vectors of head angle and stimulus angle. The gain and phase of the head roll reflex were measured (see Methods) and data were pooled from several flies (Fig. 2). Looking at the gain of the response, it is clear that a plateau value of ≈0.7 is reached at and below 1Hz, and that this does not change measurably after the ocelli are occluded. The subsequent attenuation towards higher frequencies closely resembles that of a classical low-order, low-pass filter. Towards higher frequencies, there may be a slight reduction in the gain after occlusion of the ocelli, but we think that the overall effect may be masked somewhat by the large variation in gain we observed from single animals. The root cause of the larger variation in gain is unclear, but we believe it may be related to spontaneous changes in the behavioural 'state' of the animal which are seen in the head movements of tethered flying flies (Rosner *et al.*, 2009).

By comparison, the phase lag of the reflex shows a systematic increase after occlusion of the ocelli - between 10-20% across the range, with the largest increase actually occurring at the lower frequencies (despite the appearance of the graph in Fig. 2). Phase lag reaches 90° at 8Hz (without ocelli) or 9Hz (with ocelli), at which point the gain is ≈0.25. Beyond this, we even observed a sizeable response at 20Hz (≈0.2 with ocelli) however, at this frequency the system is almost fully into positive feedback (phase lag: 160°). Though such a relatively high gain in the positive feedback region might seem nonsensical, we feel it is important to note here that the visually-mediated reflex ordinarily does not operate in isolation, without input from the fly's mechanosensory systems. The compound reflex (visual + mechanosensory) performs much better at these frequencies (described later in this report). Despite this, it would be sensible to assume that the fly could still benefit from a lower corner frequency, or a sharper cut-off for the visually mediated reflex, and it might be a fruitful line of investigation to assess why this is not this the case.

The phase of the reflex is helpful in assessing the performance, but it also essential to know the absolute latency of the fly's head roll movements with and without the ocelli. We calculated the latency via two methods, one is a conversion from the phase data (Fig. 3A) and the other was obtained directly through temporal cross-correlation (Fig. 3B - see Methods). These data highlight that the largest performance gains mediated by the ocelli are at the lower frequencies. The plots also clearly show how the latency of the reflex drops substantially as the frequency of the stimulation increases, to what must be considered a near-minimum value of ≈20ms.

As a control experiment, we varied the amplitude of our sinusoidal stimuli between 10° and 30°, and again calculated the gain, phase and latency of the headroll reflex. A small but systematic change in all three parameters was observed, across the frequency range (2 flies, n=28). Firstly, the gain of the response apparently increases as the amplitude of the stimuli decreases (Fig. 4). This inverse relationship may in part be a real effect, perhaps due to increasing mechanical resistance as the head rotates to larger angles, or increasing muscular fatigue. However, we think it is more likely an artefact due to the underlying noise distribution in the head position data. The noise has two sources: real, but stimulus-uncorrelated (random) roll motion of the head, and random positional errors introduced by the automated video analysis software. The noise should follow an approximate Gaussian distribution, so will contain some power in *all* frequencies at random phases - including that of the stimulus waveform. As the stimulus amplitude is lowered, the response S/N ratio falls, and so the gain appears to increase at all frequencies. This is perhaps why we observe that the gain is greater by ≈0.1 at 10° amplitude than at 30°.

While the gain apparently increases with decreasing stimulus amplitude, the phase and latency show substantial decreases (Figs. 4 & 5). It is unclear why we observe this marked reduction (up to 20ms/20°) in the latency and phase at lower stimulus amplitudes. The effect is less likely to be due to reduction in S/N ratio, because the phase of the frequency components of the noise distribution is random, and so should not change the apparent phase of the response waveform. Interestingly,

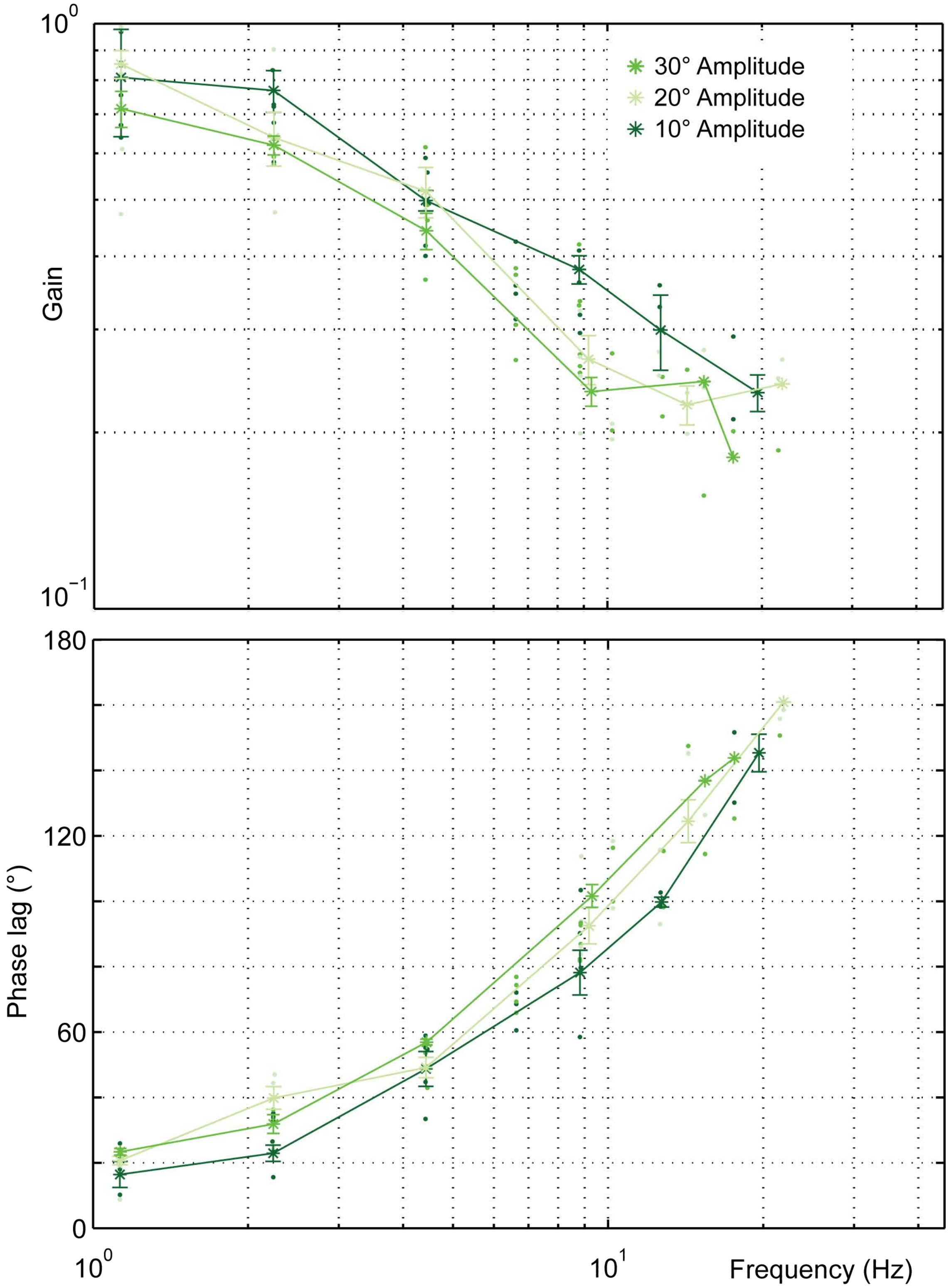

Figure 4: Bode plot of compensatory headroll, for 3 different stimulus amplitudes (2 flies, n=28). The gain and phase were calculated for experiments performed at 10°, 20° and 30° amplitude (20°, 40° and 60° peak-to-peak). Both visual systems were operational during these experiments.

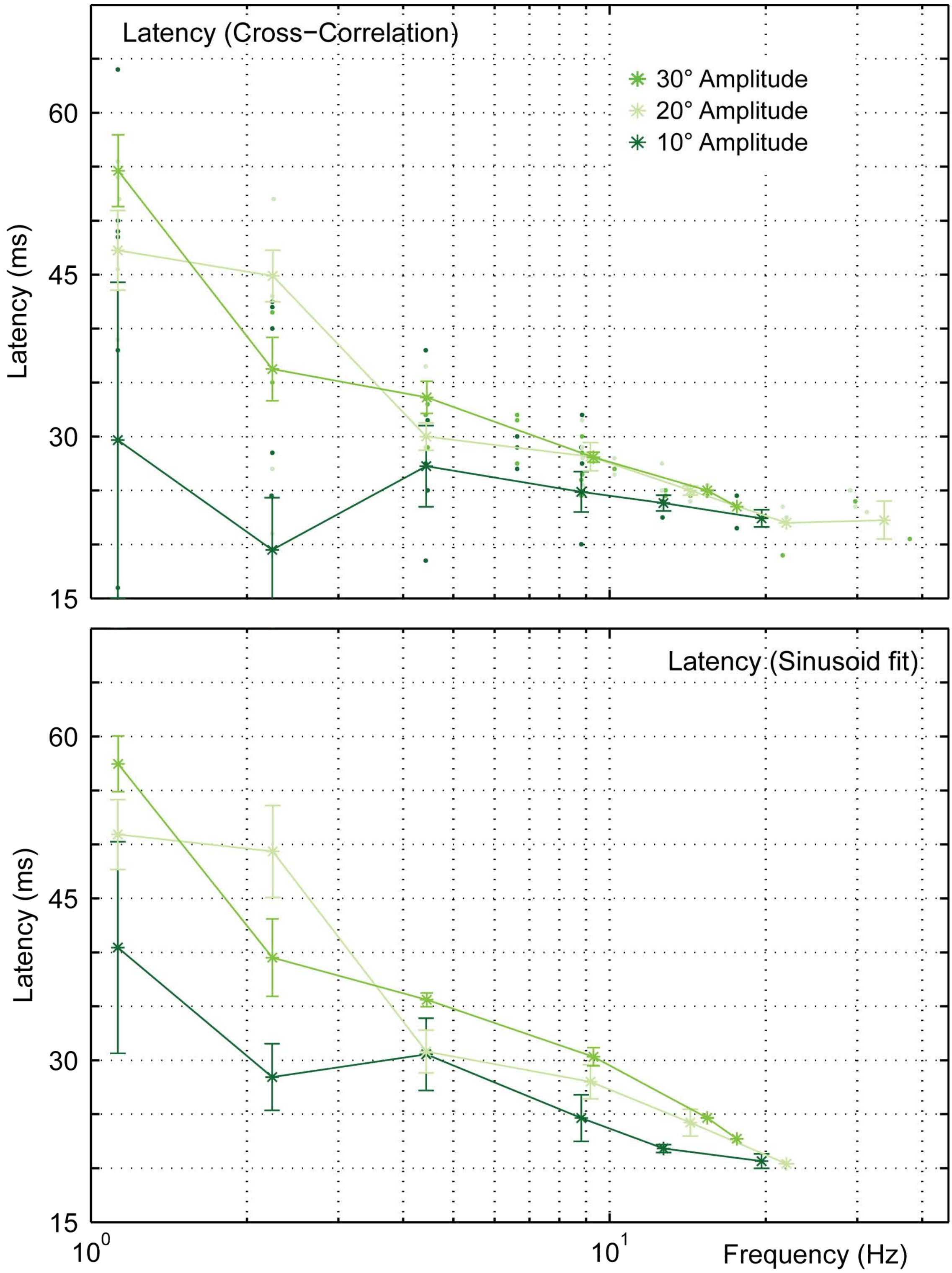

Figure 5: Response latency of compensatory headroll, for 3 different stimulus amplitudes (2 flies, n=28). The gain and phase were calculated for experiments performed at 10°, 20° and 30° amplitude (20°, 40° and 60° peak-to-peak). Both visual systems were operational during these experiments.

both the phase and latency at 10°, 20° and 30° amplitude converge at ≈20Hz, whereas the gain does not. They converge at the minimum possible latency for the visually-guided headroll reflex (20-25ms), which implies that this is a real effect, rather than some spurious measurement, since it doesn't affect all frequencies equally, and seems to obey a physical constraint. We can think of two possible reasons for the effect. Firstly, note that the maximum angular velocity of the stimulus is directly related to the amplitude of the stimulus (the maximum gradient of a sinusoid is $2\pi Af$, where A is the amplitude, and f the frequency). Therefore at higher amplitudes the head will also be rotating faster to keep up with the stimulus, with an associated increase in inertia. This added inertia might substantially increase the time taken for deceleration and subsequent acceleration during direction reversal. Secondly, at lower amplitudes, most of the visual stimulation is occurring close to the dorsal/ventral midline of the compound eyes - as the amplitude increases, the stimulation is spread out across a larger area around the midline. It remains to be seen whether there is enhanced sensitivity to motion close to the horizon. However, from what we know of the physiology of the VS-neurons (Krapp *et al.*, 1998) the axons of these cells are generally within the area of the lobula plate which receives input from the equatorial region of the compound eye - this could be a contributing factor to the change in latency.

4.2 Step response of visually-mediated headroll reflex

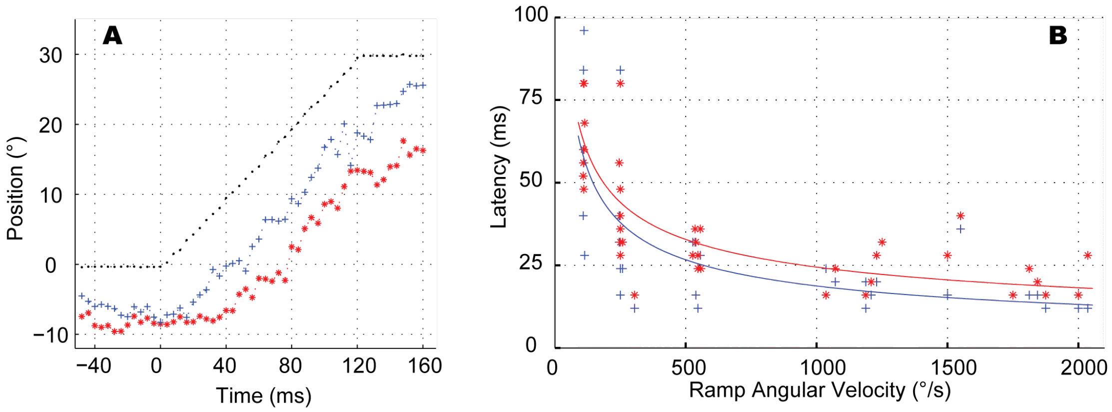

Figure 6: Head movements during ramp stimulation of varying angular velocity. **A:** Head position (blue: ocelli operational, red: ocelli disabled) during ramped change in position of stimulus hemisphere (black), angular velocity: $250°/s$ (1 fly, n=14). **B:** Latency (hand-measured, $\pm 4ms$) at a range of ramp velocities, from 100-2000°/s. Solid lines show least-squared fits of the form $y = A + Bx^C$ (2 flies, n=21)

The latency values we have presented so far are essentially dynamic latencies - either calculated via cross correlation, or from the phase of the response waveform. To obtain a more traditional measure of the latency ('static' latency) we stimulated tethered flies with a series of constant-angular velocity steps of the stimulus. These ranged in angular velocity from 100-2000°/s, and were of either 30° or 60° amplitude. There was quite some variation in the time course of the headroll response to a step change in the stimulus position, but on average the motion of the head followed the stimulus with a constant angular velocity and a small delay (Fig. 6A). At higher stimulus angular velocities, the head would not reach the same velocity as the stimulus, suggesting that the limit to the force which the neck muscles can generate might be reached below angular velocities of 2000°/s. However, further experiments - including stimulation of the halteres - would be required to ascertain the position of this limit.

We measured the latency of the step response (see Methods) at each step velocity from 100-2000°/s (Fig. 6B). In a somewhat analogous manner to the phase and latency values presented earlier, the latency of the step response drops off quite rapidly as the angular velocity increases, and reaches an apparent minimum value of ≈13ms at around 2000°/s. If the ocelli are occluded, latencies are on average increased across the angular velocity range, and the minimum value is close to 20ms. The stimulus protocol consisted of a long 'train' of individual steps, so that starting angular position and direction of the steps could be varied along with the amplitude and angular velocity (Fig. 7A). This

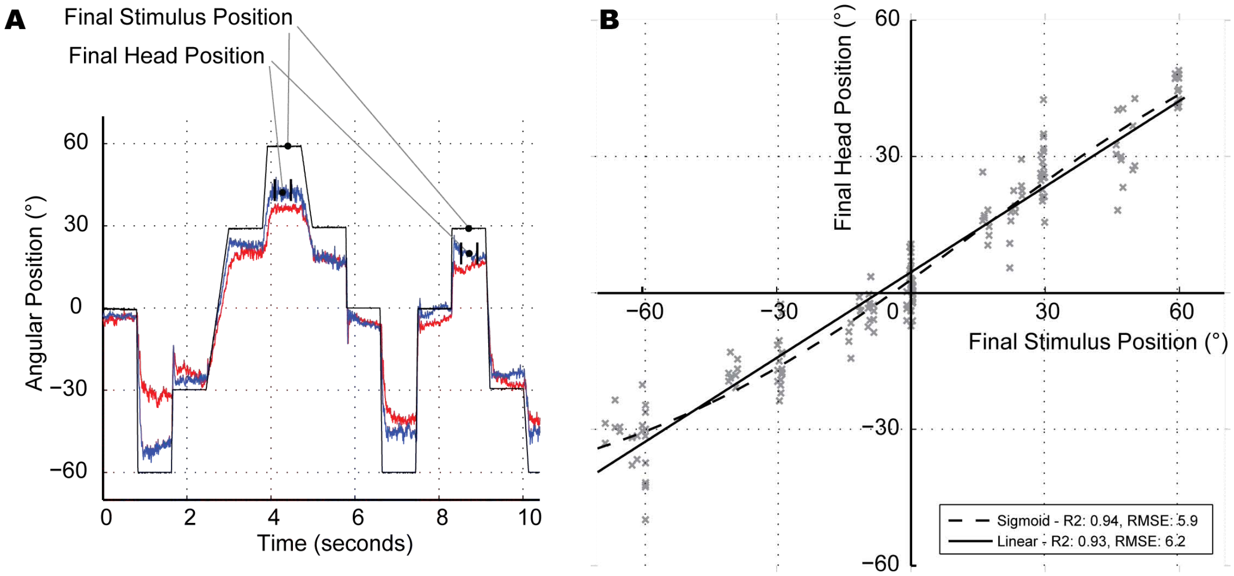

Figure 7: Head movements during trains of ramps of varying amplitude, position, direction and angular velocity. **A:** 10-second portion of ramp train, illustrating the final positions of the stimulus and the head - these were calculated by averaging the position over the central 50% of points between pairs of ramps. **B:** Final head position (y-axis) plotted against final stimulus position (x-axis) (3 flies, n=31). Solid and dashed lines show linear and sigmoid least-squares fits to the data, respectively. Data were obtained from flies both with ocelli operational, and with ocelli disabled.

generated an interesting result, in that the starting position of the stimulus seemed to have a greater bearing on the amplitude of the head roll response than did the velocity or amplitude of the stimulus (Fig. 7B). Although the amplitude of the response was generally less than the amplitude of the stimulus, the 'gain' was much closer to 1 when the final head position was within the range -30° to 30°, than when the stimulus moved towards larger head positions. We are not able to draw any firm conclusions regarding this effect at present, as it is unclear whether the reluctance of the head to move towards larger angular deviations is somehow due to our experimental paradigm. Furthermore, it may be that the addition of mechanosensory input is necessary for the headroll reflex to extend out towards the full range. Finally, there was negligible difference in the final head position whether the ocelli were operational or occluded. This fits well with what we know of the phasic nature of ocellar L-neurons (Simmons *et al.*, 1994) and that the dorsal light reflex in the post-stimulus range of 500-1000ms is mediated almost exclusively by the compound eyes (Schuppe & Hengstenberg, 1993).

4.3 Frequency response with mechanosensory stimulation

Recently we added an extra dimension to our tethered flight stimulator by introducing stimulation of the fly's mechanosensory systems (primarily the halteres - see Methods). We measured the headroll response in a similar manner to before (condition C1), but with sinusoidal roll stimulation of the fly (ego-motive paradigm - see Methods). As before, the ocelli were occluded, and the experiments were repeated (condition C2). Then, with the ocelli still disabled, the halteres were cut very close to their base, so that they were still able to beat as before, but would not generate any signals related to the coriolis force (condition C3). In this way, wingbeat-synchronous ascending input from the halteres (known to gate visual input to motor neurons (Huston & Krapp, 2009)) was probably preserved, but the halteres would definitely no longer directly contribute to the headroll reflex. These data highlight the great performance advantage mediated by the the halteres. In conditions C1 & C2, the high-performance region of the headroll reflex extends up to 6-7Hz, and the reflex is heading towards positive feedback at a probable 30Hz (we only measured up to 15Hz). In condition C3 (halteres and ocelli disabled), the high performance region of the headroll reflex extends only up to 2-3Hz, and the reflex enters positive feedback at 8-9Hz. Note that with the halteres disabled, the gain and phase of the headroll reflex are remarkably similar to that measured with the ego-static paradigm (Fig. 8). This

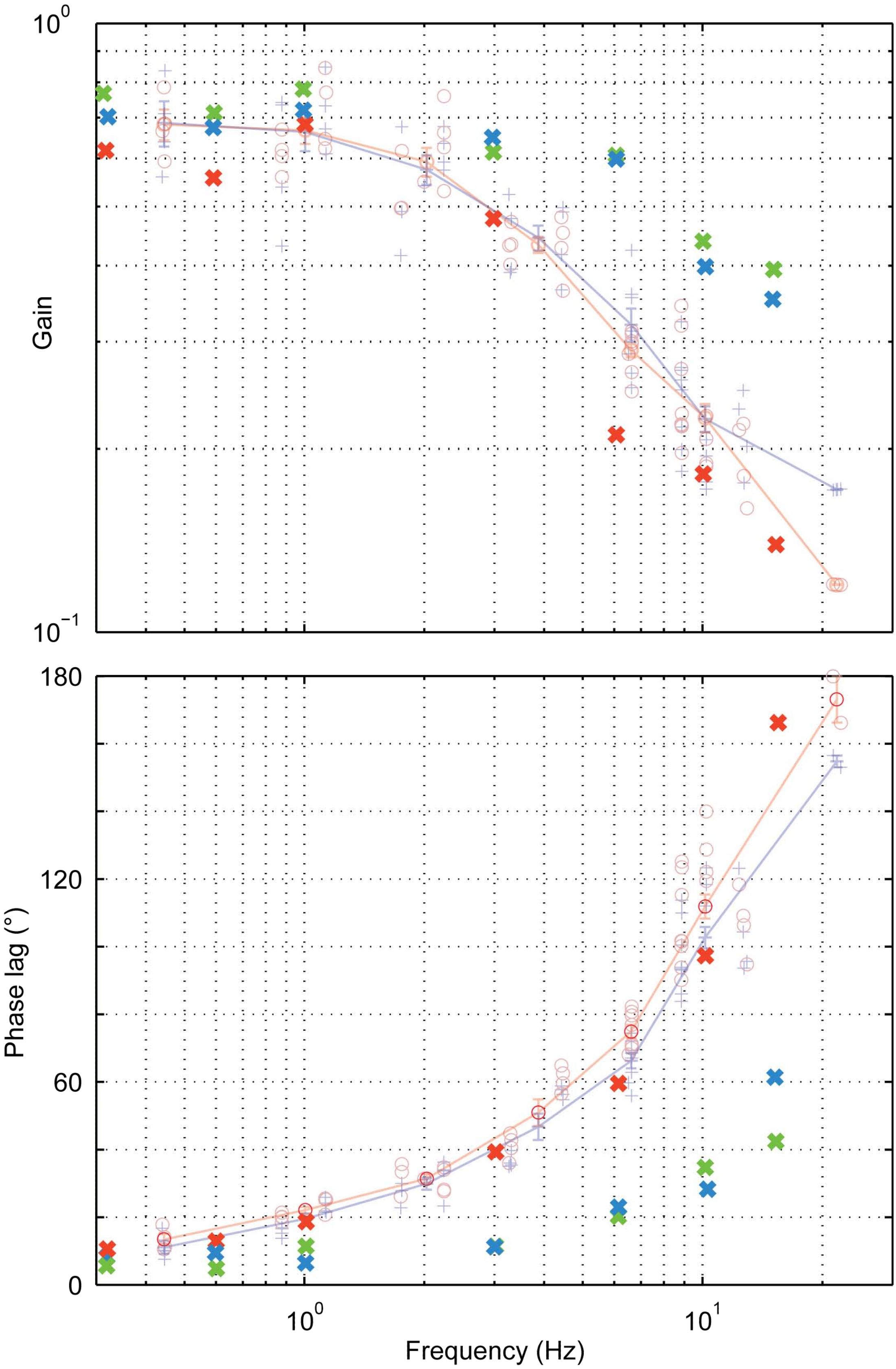

Figure 8: Bode plot of visual and haltere-mediated compensatory headroll movements (3 flies). The coloured crosses mark data obtained with ego-motive stimulation (Fig. 1), compared with the data obtained with ego-static stimulation (same as Fig. 2). The different coloured crosses describe three behavioural conditions, C1 (green), C2 (blue) and C3 (red). In C1, all sensory systems are operational; in C2, the ocelli are disabled; in C3, the ocelli are disabled, and the halteres have been surgically removed (see Methods).

suggests that the halteres are the only sensory system involved in gaze stabilisation other than the ocelli and compound eyes, despite a previous study which stated that there is a component mediated by wingload sensors (Hengstenberg, 1993).

5 Conclusions

Our results show that the fly gaze stabilisation reflex in general has the properties of a low-pass filter - the shape of the gain and phase plots illustrate this perfectly. However, as our later experiments involving the halteres show, two parameters of the filter - corner frequency, cut-off - are not defined by the motor system, but change according to the available sensory information. Low-frequency performance is maintained through sensory input from the compound eyes, while the addition of sensory input from the halteres smoothly extends the range of the reflex to much higher frequencies. Interestingly, sensory input from the ocelli gives a small advantage across the entire frequency range whereas, given the phasic nature of ocellar inputs to VS neurons, we would have expected little or no difference at frequencies where the period of the waveform approaches $\geq$500ms (Simmons *et al.*, 1994). In general however, the size of the reduction in latency of the headroll reflex with ocellar input matches what we would expect from our previous electrophysiology experiments (Parsons *et al.*, 2006, 2010).

Our data perfectly complement those of Hengstenberg, Hengstenberg & Schuppe (Hengstenberg, 1993; Schuppe & Hengstenberg, 1993). In these earlier studies, the authors characterised the headroll reflex in terms of sensitivity at different angular velocities of motion. Here we have described the reflex in terms of frequency response - these data are essential so that we can begin to model the fly's control system with a firm grasp of the real physical parameters. Now we have a more complete picture of the filtering properties of the entire reflex, as well as the individual sensors - the compound eyes, ocelli and halteres - the next step in this process will involve measuring some of the physical properties of the motor system, while further probing the integration of sensory signals at the motor neuron level. While continuing to expand our description of the headroll reflex, we also intend to extend our study to the fly's body stabilisation reflex. The dynamics of whole-body stabilisation are completely different to those of head stabilisation, so we would expect this to be reflected in the frequency response of the flight stabilisation reflex.

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