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# Vision-based flight control and stabilisation in hawkmoths

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Thesis submitted in partial fulfilment of the requirements for the Degree of  
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*To my sister Dolphine, whose willpower  
and persistence are a constant source of inspiration.*

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# Vision-based flight control and stabilisation in hawkmoths

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## Abstract

Insects are inherently unstable and therefore rely on sensory feedback in order to maintain flight control and stability. This thesis focuses on how the hawkmoth *Manduca sexta* uses visual feedback to control and stabilise flight. The analysis is based on extensive sampling of the optomotor responses. I use a virtual reality flight simulator to measure the total moment that the moths generate in response to oscillating wide-field stimuli. The visual stimuli simulate rotations of different amplitudes and frequencies about six different body axes. The moment responses depend upon stimulus amplitude, so are fundamentally non-linear. Nevertheless, for a fixed and suitably small stimulus amplitude, it is possible to fit a linear PID-controller with time delay to each of the optomotor responses. The analysis shows that the moths rely on proportional and integral feedback of angular velocity, with different time delays about different rotation axes. This varying time delay prevents spatial superposition of the optomotor responses to lateral rotational stimuli, meaning that there is no general control law that predicts the responses to an arbitrary lateral stimulus. By combining these empirically derived vision-based flight controllers with linearised flight dynamic models of hovering *M. sexta*, I evaluate their performance in providing flight stability. This analysis suggests that visual feedback is sufficient to stabilise disturbances associated with rotational stimuli about the horizontal roll and dorso-ventral axes, but is insufficient to stabilise disturbances associated with rotational stimuli about the pitch axis, vertical yaw axis, and longitudinal body axis. The time delay of the optomotor response has a substantial influence on the superposition of the measured optomotor responses, and strongly affects the predicted flight stability. The findings presented in this work have implications for understanding not only the mechanisms and functionality of flight control in hawkmoths, but also the results of past and future investigations into vision-based flight control in insects and flapping-wing air vehicles.

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# Nomenclature

## Roman Symbols

|                |                                                                                                      |
|----------------|------------------------------------------------------------------------------------------------------|
| $\mathbf{A}$   | system matrix representing the passive flight dynamics                                               |
| $A$            | stimulus amplitude                                                                                   |
| $\mathbf{A}_c$ | control matrix                                                                                       |
| $E(s)$         | Laplace transform of the input signal $\epsilon(t)$                                                  |
| $f$            | temporal frequency                                                                                   |
| $f_c$          | contrast frequency                                                                                   |
| $H(s)$         | transfer function that describes the linear transformation from the visual input to the motor output |
| $K_D$          | control gain proportional to the time derivative of the input signal $\epsilon(t)$                   |
| $K_I$          | control gain proportional to the time integral of the input signal $\epsilon(t)$                     |
| $K_P$          | control gain proportional to the input signal $\epsilon(t)$                                          |
| $L$            | roll moment response about the horizontal x-axis                                                     |
| $M$            | pitch moment response about the y-axis                                                               |
| $N$            | yaw moment response about the vertical z-axis                                                        |
| $p$            | angular rate for oscillations about the horizontal x-axis                                            |
| $p'$           | angular rate for oscillations about the longitudinal x'-axis                                         |
| $p''$          | angular rate for oscillations about the x''-axis                                                     |

## *Nomenclature*

|                 |                                                                            |
|-----------------|----------------------------------------------------------------------------|
| $q$             | angular rate for oscillations about the y-axis                             |
| $r$             | angular rate for oscillations about the vertical z-axis                    |
| $r'$            | angular rate for oscillations about the dorso-ventral $z'$ -axis           |
| $s$             | complex frequency                                                          |
| $U(s)$          | Laplace transform of output signal $u(t)$                                  |
| $u(t)$          | output signal of the optomotor system, i.e. the measured moment response   |
| $\mathbf{x}$    | predictor matrix                                                           |
| $\mathbf{x}(t)$ | state vector                                                               |
| $x$             | body axis aligned with the horizon and within the moth's plane of symmetry |
| $x'$            | longitudinal body axis within the moth's plane of symmetry                 |
| $x''$           | axis at $45^\circ$ intermediate to the x-axis and the -y-axis              |
| $y$             | the moth's transverse principal axis, pointing out along the right wing    |
| $z$             | body axis aligned with gravity and within the moth's plane of symmetry     |
| $z'$            | dorso-ventral body axis within the moth's plane of symmetry                |

### **Greek Symbols**

|               |                                                                           |
|---------------|---------------------------------------------------------------------------|
| $\epsilon(t)$ | input signal of the optomotor system, i.e. the visual stimulus            |
| $\phi$        | angular position of a roll stimulus                                       |
| $\psi$        | angular position of a yaw stimulus                                        |
| $\gamma$      | horizontal angle between the moth's head and the feeder, i.e. the azimuth |
| $\theta$      | angular position of a pitch stimulus                                      |

### **Acronyms**

|     |                |
|-----|----------------|
| CoM | centre of mass |
|-----|----------------|

## *Nomenclature*

|      |                              |
|------|------------------------------|
| EMD  | elementary motion detector   |
| LCT  | linear control theory        |
| LPTC | lobula plate tangential cell |
| LTI  | linear and time-invariant    |
| RGA  | Relative Gain Analysis       |
| WBA  | wingbeat analyser            |

# Chapter 1

## Introduction

### 1.1 Context

Insects fly through a multitude of environments, ranging from fields of flowers, to woods, to rooms with comparatively blank walls. They are also constantly subject to unpredictable circumstances such as objects intersecting their flight path, gusts and turbulences, or predators. In short, their visual environment changes a lot and insects need to perform rapid manoeuvres, adapt and respond quickly to secure their survival. An impressive array of sensors provides the insect with information on its environment and also with information on its self-motion in the three-dimensional space. Knowledge on its environment is crucial for navigation and guidance and will drive behaviours such as chasing, evasion, object avoidance and feeding. Knowledge of its self-motion on the other hand, is key to flight control and stabilisation. The aim of this thesis is to identify the role of visual sensory feedback in flight control and stabilisation. Flight stabilisation is an insect's ability to counteract and reject disturbances and to regain a stable attitude in space.

## Chapter 1 Introduction

I am using the tobacco hornworm hawkmoth *Manduca sexta* (Lepidoptera: Sphingidae) as my model system. There are three main reasons for this choice: Firstly, its comparatively large body weight means that it produces large aerodynamic forces and moments, which therefore have a good signal to noise ratio when measured on a force balance. Secondly, it hovers in front of flowers to feed, and can consequently be persuaded to fly when tethered, without having to provide an oncoming airflow. Thirdly, it is a widespread model system used for investigating neurobiology and flight mechanics and supplementary information on *M. sexta* can therefore be drawn from multiple sources.

In order to analyse vision-based flight control and stabilisation in *M. sexta* I first measure how the moth's flight behaviour varies with the spatial and temporal variation of the rotational visual stimuli. Based on this extensive data set I then assess the control laws that describe how and with what time delay visual information is transformed to a behavioural response. I will also explore whether these vision-based flight control laws provide sensory information sufficient to stabilise the flight of a hovering moth.

From a biological perspective this study of the motion vision pathway sheds light on how the motion vision pathway and the flight apparatus may have co-evolved to provide stability within the constraints imposed by the limited speed of sensorimotor processing, the inherent instability of the moth, and the need for rapid and robust responses to unpredictable circumstances. Hence, I will discuss whether the visual system displays a particular sensitivity to particular classes of apparent body motion which would excite inherent instabilities in the moth's flight dynamics if left uncorrected.

In this thesis I make use of the control models commonly used in linear control theory and abstract the motion vision signal processing of a natural flier to a level which is approachable for technical implementation. From an engineering perspective, this study could be of interest for multiple reasons. It discusses the significance of the spatiotemporal

sensitivity of the visual sensory components to assess the vehicle’s self-motion. The fitted vision-based flight control models indicate how visual feedback could be implemented into the flight control loop. And, this study shows that moths rely on multiple time delays in the sensorimotor pathway. This variation in time delay could either improve flight stability for different body rotations or it may improve sensory fusion. A vision-based flight control algorithm could enhance the capability of onboard cameras and could potentially circumvent the need for computationally intensive estimation of the vehicle’s attitude. The vision-based control mechanisms observed in the natural flier could allow technical fliers to operate across a larger range of dynamic input. Hence, it would allow greater manoeuvrability and robustness of the vehicle in dealing with unpredictable disturbances and changing environments.

## 1.2 Optomotor responses

In this thesis I evaluate the role of visual feedback in flight control and stabilisation by measuring the optomotor response. The optomotor response is a widely used experimental paradigm which I will refer to very often throughout this thesis. The optomotor response is a motor response that insects generate when exposed to a visual stimulus with the aim of stabilising the insect’s orientation with respect to its environment [1]. For instance, if an insect is veered off to the right, the optic flow (i.e. the image motion on the eyes) will move to the left. As a consequence, the insect will turn to the left to minimise optic flow and compensate for the undesired body motion. Two very common methods for measuring this motor response are the wingbeat analyser (WBA), and high-speed videography. In the WBA, a *Drosophila melanogaster* is tethered at the centre of an array of LED panels, below an infrared light source [2]. As the fly changes its flight behaviour in response

## *Chapter 1 Introduction*

to visual stimuli, it changes the shadow it casts onto an infrared sensor. Hence, the optomotor response is quantified by the change in wingbeat frequency and the difference in stroke amplitude between the left and the right wing. Because of the way that visual stimuli are provided and because of how the motor response is measured, this setup is mostly used to study yaw and thrust kinematics during stripe fixation, object avoidance and landing responses [3] [4] [5]. Except, Theobald et al. [6] used the WBA to study the optomotor response to optic flow fields about three cardinal axes and found that the dynamics of stabilisation varied for the different types of perturbations. High-speed videography is usually used in combination with either wind tunnels or free flight arenas, where the behavioural change is quantified by the insect's six degree of freedom motion and by its wingbeat kinematics [7] [8]. The disadvantage of free flight experiments is that the visual stimulus cannot be clearly defined. In this thesis I do not measure the kinematic responses until the experimental chapter 6, but instead I tether the moth to a force balance and directly measure the forces and moments that they generate for the different spatiotemporal compositions of wide-field rotating panorama. It is generally assumed that the physiology is not affected by tethering the insect and that the visual sensory input is processed to a motor output in the same way as it would be in free flight [9]. All of the above methods (i.e. the WBA, high speed videography, force balance) allow the mapping of visual sensory input to motor output, independent of how the motor output is measured. In order to quantify the feedback of visual cues and the time delay of the system, I fitted the optomotor responses with controllers commonly used in systems engineering and hereby derived the vision-based flight controllers. The optomotor responses discussed above differ from what engineers commonly think of as a controller, because they include the effects of muscle activation. In engineering, the controller only transforms the sensory input into a control signal that is then passed on to the actuators.

Nonetheless, it is convenient to model the optomotor system as a black box (figure 1.1), with the visual stimulus  $\epsilon(t)$  as input and the motor response  $u(t)$  as output, in order to then perform a system identification and characterise the flight control strategies.

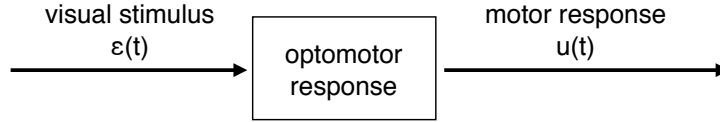


**Figure 1.1:** The optomotor system lumps the visual system and the muscle actuators into one. Hence, the optomotor system is approximated as a black box with the visual stimulus  $\epsilon(t)$  as input and the motor response  $u(t)$  as output. The optomotor response is defined as the dynamic relationship between the motor response and the visual input.

In order to understand the optomotor response one needs to understand the visual system and its properties. In the next step, I therefore briefly explain two main components: the elementary motion detectors (EMDs) and the wide-field motion-sensitive and direction-selective interneurons. As will become clear in chapter 3, the sensitivity of these components to the spatiotemporal properties of the visual stimuli is manifested at the level of the flight behaviour and thereby indicates their importance to flight control and stabilisation.

### 1.2.1 Mechanisms and components of the compound eye

#### Elementary motion detectors

When the insect moves through the world, the scenery is transformed onto the retina as a temporal sequence of brightness values called the contrast frequency [10]. As shown in equation 1.1, the contrast frequency  $f_c$  is the ratio of the mean velocity of motion  $v$  and the spatial composition of the scenery represented by the spatial wavelength  $\lambda$ .

$$f_c = \frac{v}{\lambda} \quad (1.1)$$

The most common model for biological motion detection is the non-linear correlation-type elementary motion detector (EMD), or the Hassenstein-Reichardt detector [11] [12]. This type of EMD compares the temporal change in brightness values across neighbouring ommatidia. Its direction-selective output indicates the magnitude of relative motion at a given location in the visual field. As shown in figure 1.2, its response increases with image velocity  $v$ , reaches a maximum, and drops again. Hence, its response is ambiguous with respect to velocity if the velocity is allowed to exceed the range over which the response is monotonically increasing with velocity. The ambiguity is made more complicated because the location of the velocity maximum varies with spatial wavelength  $\lambda$ . As illustrated in figure 1.2, sinusoidal gratings with different spatial wavelengths cause the EMD to be sensitive to a lower or higher range of image velocities, such that the ratio of the optimal velocity and the spatial wavelength, i.e. the contrast frequency  $f_c$ , remains constant [1]. Hence, EMDs are tuned to a contrast frequency and therefore their response depends on motion amplitude  $A$ , temporal frequency  $f$ , spatial wavelength  $\lambda$ , and image contrast and brightness [13]. The EMDs are assumed to be tuned to have a monotonically increasing response over the entire range of speeds encountered naturally. Reviews: [14] [15].

### **Wide-field motion-sensitive and direction-selective interneurons**

The local motion vectors measured by the EMDs are ambiguous with respect to the self-motion that caused them. As shown in the shaded areas of the optic flow fields in figure 1.3, local motion vectors can point in the same direction although the insect is undergoing different types of self-motion such as lift translation or roll rotation.

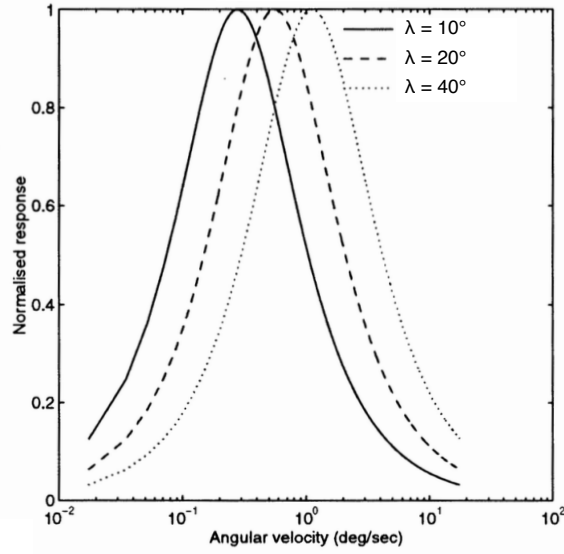


**Figure 1.2:** Characteristic velocity tuning curve of a correlation-type elementary motion detector for sinusoidal gratings of different spatial wavelengths  $\lambda$ . The consequence of using a spatiotemporal correlation for motion detection is the sensitivity of the detector to contrast frequency. Hence, the peak response of the detector is generated for a particular contrast frequency  $f_c$ , i.e. the ratio of image velocity  $v$  over spatial wavelength remains constant. As a consequence, the velocity optimum shifts to lower values if the spatial wavelength  $\lambda$  is diminished (i.e. thinner stripes). Conversely, the velocity optimum of the EMD shifts to higher values if the spatial wavelength is increased (i.e. thicker stripes). Figure adapted from Srinivasan et al. [1].

In order to overcome this ambiguity, the output of the EMDs is spatially integrated across subareas of the visual field to form optic flow fields similar to those shown on the right in figure 1.3. These optic flow fields represent an internal mapping of the retinal shift that insects experience due to self-motion. They are essential to flight stabilisation because they contain information on the translational and rotational motion of the insect. This spatial integration is performed by wide-field motion-sensitive and direction-selective interneurons. They are direction-selective because they are excited by motion in their preferred direction and are inhibited by motion opposing their preferred direction. Hence,

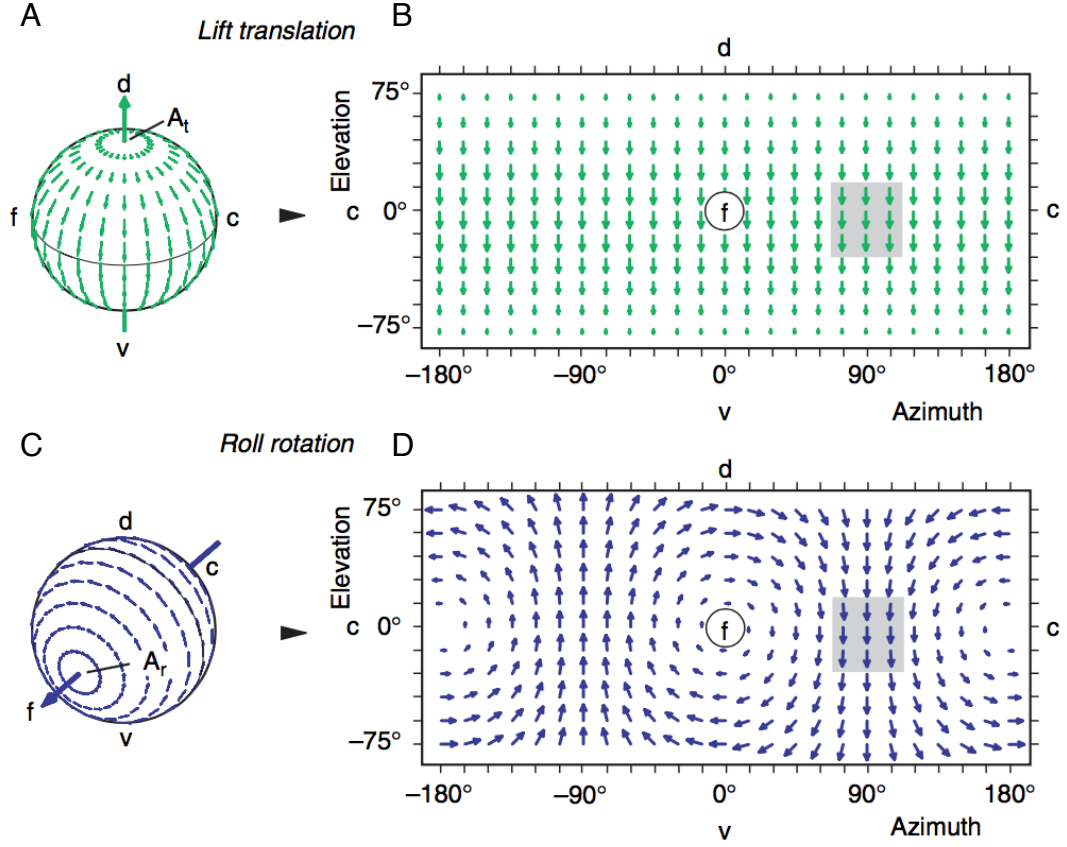


**Figure 1.3:** Optic flow fields induced by upwards lift translation (A and B), and by a roll rotation to the left (C and D). The arrows indicate the local retinal image shift at different positions within the hexagonal eye lattice ( $f$ , frontal;  $c$ , caudal;  $d$ , dorsal;  $v$ , ventral). The schematics in A and C illustrate the optic flow on the surface of the visual unit sphere.  $A_t$  (in A) is the axis of body translation.  $A_r$  (in C) is the axis of body rotation. The schematics in B and D illustrate the optic flow in a cylindrical projection where  $f$  indicates the frontal position directly in front of the insect. The grey area in the right visual hemisphere at an elevation of  $0^\circ$  and at an azimuth of  $90^\circ$  shows that at the local scale, the direction of the local motion vectors is ambiguous. We only see the differences in optic flow caused by lift translation and left roll rotation when the visual information is integrated across a larger section of the visual field, i.e. we only see the difference in optic flow patterns when we look at the global scale. Figure adapted from Krapp et al. [16].

## Chapter 1 Introduction

they generate a maximal response if the optic flow field matches the preferred pattern of optic flow for this particular interneuron. In flies, these wide-field motion-sensitive and direction-selective interneurons are located in a particular area of the third visual neuropile called the lobula plate and are therefore referred to as lobula plate tangential cells (LPTCs). Reviews: [17] [18] [19] [20] [21] [14] [22] [23].

*M. sexta* is a crepuscular species and in contrast to the diurnal Diptera which have been used for the majority of optomotor flight control studies, it lacks halteres and functional ocelli [24] [25]. Hence, *M. sexta* are missing two key sensory modalities that provide very fast feedback for rapid course corrections [23] [26]. Halteres are gyroscopic sensors and feed back inertial information with very short time delays. Ocelli are visual sensors located on the top of the head and feed back rapid changes of roll and pitch motion, measured from the deviation to the horizon. Additionally, *M. sexta* have a versatile flight behaviour as they can fly over large distances, hover and fly backwards. Studies of nocturnal and crepuscular species discuss the tradeoff between the larger integration time that these species require to provide information with a good signal to noise ratio, and the fast feedback that the system requires in order to maintain stability [10] [27] [28]. O’Carroll et al. [10] and Wicklein et al. [29] studied the spatio-temporal properties of wide-field motion-sensitive and direction-selective interneurons in the lobula complex of the diurnal hummingbird hawkmoth *Marcoglossum stellatarum*. There are also two studies of wide-field motion-sensitive interneurons in the lobula complex of *M. sexta*: Wicklein et al. [30] characterized classes of neurons that responded to expanding and contracting retinal images. While Theobald et al. [27] found that the response of wide-field motion-sensitive neurons peaked for sinusoidal gratings with a spatial frequency of 0.074 cycles/° and moving with a temporal frequency of 2 Hz.

The output of the visual system is passed on to descending motor neurons where it is

integrated with feedback from other sensory modalities. Using intracellular recordings, Sprayberry [31] reported that object-sensitive descending neurons in *M. sexta* (i.e. neurons located at a stage where the information from the optic lobes is likely to have merged with feedback from other sensory modalities) respond to dummy flowers oscillating at frequencies as high as 6 Hz with latencies of 40-90 ms.

Based on the studies mentioned above, it seems safe to assume that *M. sexta* will also have neurons which are tuned to particular patterns of optic flow and hence, play a key role in the flight control and stabilisation. One question which I address in this thesis is whether this pattern sensitivity is related to the flight dynamics (as suggested by the mode sensing hypothesis discussed in the next section [23]). I also ask if and how the signals from these individual wide-field motion-sensitive and direction-selective interneurons are recombined to generate a control signal (which I address by testing spatial superposition in chapter 4).

### 1.3 Flight dynamics

The mode sensing hypothesis developed by Taylor et al. [23] suggests that sensorimotor responses are matched to the system they are controlling. Hence, it suggests that the sensory system has evolved to accommodate the flight dynamic properties of the insect. This hypothesis motivates the consideration of the optomotor responses in the context of their flight dynamics. Flight dynamics represent all of the flight physics, and are described by equations of motion that explain the relationship between the insect's body dynamics and the forces and moments that produce them. The flight dynamics relate partly to the inertial properties of the insect but conventionally also include the direct aerodynamic effects of the insect's motion on the aerodynamic forces and moments.

## Chapter 1 Introduction

In a technical flyer, the controller and the flight dynamics can be separated into two distinct components, whereby the flight dynamics are usually referred to as the plant. In insects on the other hand, this separation of controller and flight dynamics is a theoretical abstraction (albeit a very useful abstraction) because unlike technical flyers, we cannot distinguish the insect's flight dynamics in the absence of control. This is resolved by approximating the insect's flight dynamics using numerical flight simulations. There are large number of studies of insect flight dynamics that employ different levels of complexity in dealing with the highly non-linear aerodynamics of a flapping wing body [32] [33] [34] [35] [36] [37] [38] [39] [40]. Nonetheless, these studies uniformly show that insects are inherently unstable and therefore rely on sensorimotor responses to control and stabilise flight.

The final aim of this thesis is to assess whether the control models that I fitted to the optomotor responses can provide stability to a hovering moth. Hence, I will combine the vision-based flight controllers with the theoretical flight dynamic studies for *M. sexta* in order to assess the stability of the closed-loop system. As shown in figure 1.4, the closed-loop system is the combination of the sensory system, the controller and the plant (i.e. the uncontrolled and inherently unstable open-loop flight dynamics). The closed-loop system essentially represents the stable flight of a moth. Because this thesis focuses on the role of visual feedback, the sensory system corresponds to the visual sensor, the controller corresponds to the controller derived from the measured optomotor responses, and the plant corresponds to the theoretical flight dynamic models of hovering *M. sexta*.

Dyhr et al. [41], Cheng et al. [42], and Windsor et al. [9] represent three studies related to my work. Each of them illustrates a different method of how an optomotor controller can be identified. Dyhr et al. analysed the visual-abdominal reflex generated in response to pitch stimuli. They fitted an optomotor controller to explain the angular deflection

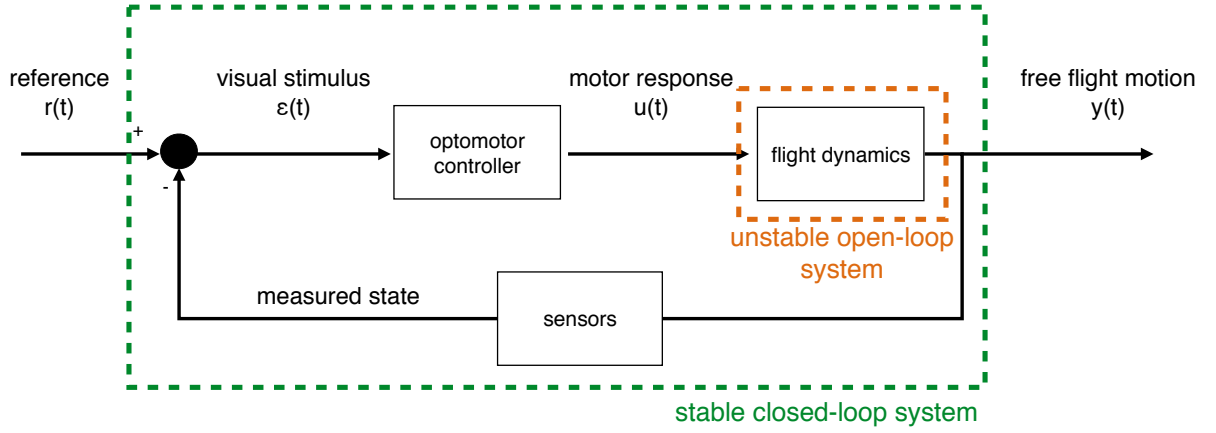


**Figure 1.4:** Schematic of the closed-loop system. The closed-loop system comprises the sensory systems, the controller and the plant. Because this thesis focuses on the role of visual feedback, the sensory system corresponds to the visual sensor, the controller corresponds to the controller derived from the measured optomotor responses, and the plant corresponds to the theoretical flight dynamic models of hovering *M. sexta*. The input to the flight controller is the visual stimulus  $\epsilon(t)$ . The visual stimulus  $\epsilon(t)$  represents an apparent motion of the body and hence, it indicates an offset from an equilibrium state  $r(t)$ . The insect compensates for the apparent motion  $\epsilon(t)$  by generating the control signal  $u(t)$ . The controlled free flight motion is described by  $y(t)$ .

of the abdomen in tethered experiments, the advantage being that the visual stimulus is clearly defined for a moth that is fixed in space. They then combined this control model with a model of the motion of the thoracic-abdominal joint of free flying moths, and concluded that the optomotor reflex barely stabilises pitch manoeuvres. Cheng et al. [42] analysed the optomotor response of *M. sexta* to a sudden frontal stimulus. They derived the open-loop flight dynamics from a dynamically scaled robotic wing and compared these kinematics to those of the closed-loop free flight responses in order to identify the optomotor controller. Windsor et al. [9] predicted the control parameters from the linearised flight dynamics model. They compared the predicted controller to the measured moment responses that *Hyles lineata* generated in response to visual roll, pitch and yaw

stimuli.

In this thesis I empirically derive the optomotor controller and combine it with existing theoretical flight dynamic models in order to analyse the stability of the closed-loop system.

## 1.4 Structure of this thesis

This thesis is structured as follows: In chapter 2, I explain the materials and methods used in the experiments with tethered *M. sexta*. These experiments were performed using a virtual reality flight simulator where I measured the total moment responses that the moths generated in response to uniaxial, wide-field oscillating rotations. This experimental rig allowed me to expand on previous investigations of optomotor responses because it allowed me to measure the total moment responses rather than being limited to a uniaxial torque measurement. Also, I could expose the moths to apparent body rotations about arbitrary axes and was not limited to providing stimuli in an orthogonal coordinate system. This allowed a thorough and extensive sampling of the aerodynamic moments that the moths generate in response to apparent body rotations. In chapter 3, I analyse the optomotor responses to roll, pitch and yaw stimuli. Based on these data I assess the linearity of the optomotor system. Testing the linearity of the optomotor system is fundamental in order to assess whether the behaviour can be observed and identified with tools and methods of the linear control theory. In chapter 4, I expand the empirical dataset to include the optomotor responses to stimuli about axes intermediate to those of pure roll, pitch and yaw. This unprecedentedly large data set of the optomotor responses forms the basis from which I derive vision-based flight control models. I then use these control models to test spatial superposition of the optomotor responses. This

## Chapter 1 Introduction

provides insight into how the control strategies may overlap or differ for different types of apparent body rotations, i.e. for different spatial compositions of optic flow. As alluded to in section 1.2.1, the spatial superposition could provide a better understanding of how the information from individual wide-field motion-sensitive interneurons is recombined to generate a stabilising response. In chapter 5, I combine the empirically derived control models with the physical model of the system. This analysis of the closed-loop system shows whether the vision-based flight controllers are sufficient to stabilise a freely hovering hawkmoth. In other words, I evaluate whether a free flying moth would be stabilised if it operated according to the flight control laws derived in chapter 4. In chapter 6, I validate the measured optomotor responses of the tethered experiments against the optomotor responses of free flying *M. sexta* to test the assumption that the response behaviour is the same. In chapter 7, I summarise the main findings of this thesis and make suggestions for future work.

The amount of empirical data discussed in this work is unprecedented in the studies of optomotor responses and allows for a broader analysis of the underlying mechanisms and functional interpretation. The way that the spatial superposition of control laws is investigated in this study is previously unreported. This is mainly due to the advantages provided by the experimental setup, where I can measure the total moment responses, and where I can simulate body rotations about arbitrary axes. Except for Windsor et al. [9], all previous studies of the optomotor system that used tethered species were limited to a uniaxial force or moment measurement which meant that a significant amount of the behavioural response was not recorded, nor included in the modelling of vision-based flight control.

## Chapter 2

# Materials and methods for the tethered experiments

In this chapter I explain the experimental work performed with tethered *M. sexta*. Using a virtual reality flight simulator, I measured the dynamic flight responses that moths generate in response to different patterns of rotating, wide-field stimuli. For the purposes of system identification, the response data is analysed in the frequency domain. The materials and methods used in the free flight experiments are explained in chapter 6.

### 2.1 Animals

Pupae of *M. sexta* were purchased from the University of Bath's laboratory colony. A total of 42 specimens of both sexes were used 2 to 4 days post-eclosion for the tethered flight experiments. In this sample of 42 moths, the females (mass:  $2.0 \pm 0.3$  g, mean  $\pm$  SD; body length:  $47.5 \pm 1.7$  mm) were generally larger and heavier than the males (mass:  $1.5 \pm 0.3$  g; body length:  $46.7 \pm 1.5$  mm). In preparation for the tethered experiments, each moth

was anaesthetised by putting it into a 4°C refrigerator prior to placing it on a cooled, 4°C manipulation stage. After removing the scales and roughening the cuticle on the dorsal surface of the thorax, the moth was fixed to an aluminium mount with cyanoacrylate glue. The mount is shaped so that the moth’s body was fixed at  $\sim 40^\circ$  pitch angle, which closely corresponds to the attitude during hovering behaviour [43]. It was then fitted to the force transducer which was located at the end of a steel arm (figure 2.2, A), such that the forward direction of the moth was aligned with the transducer’s x-axis. By lowering the steel arm, the moth was placed in the centre of a virtual-reality flight simulator, where it was left for 20 minutes before experimentation, in order for the transducer to regain thermal equilibrium and for the moth to adapt to the dimmed light levels. The moth was then exposed to the complete subset of visual stimuli selected for that particular batch.

## **2.2 Visual stimuli and flight simulator**

In order to identify the system, I needed to measure how the moth’s flight behaviour changes as a function of its apparent self-motion, i.e. as a function of the visual stimuli that I exposed them to. The behavioural changes allowed me to answer questions such as: Do the flight control parameters change with the amplitude of the apparent motion? Do they change with the rotation axis of the apparent motion? Is the response stronger for some stimuli than for others? As mentioned in the introduction, the components of the visual sensor are sensitive to the temporal and spatial composition of visual stimuli and I wanted to explore in what form this sensitivity is manifested at the level of flight behaviour, if at all. Hence, I changed the stimulus amplitude, the temporal frequency content, and the rotation axis of the stimuli. As will be explained in more detail in the respective chapters, the variation in each of these three parameters allowed me to test

for three particular properties of the optomotor system: the property of homogeneity, the property of additivity, and the property of spatial superposition. Table 2.1 shows the total of 69 stimuli that were used in the tethered experiments. Figure 2.1 shows the corresponding angular velocities.

**Table 2.1:** A total of 69 visual stimuli were presented to the moths in the tethered experiments. The stimuli vary in their temporal frequency (double-sine and single-sine waveforms), in their amplitude, and in their spatial composition (i.e. the oscillation is presented about six different rotation axes). Hence, the stimuli are divided into three sets, whereby each set is designed to test a specific property of the optomotor system. The variation in stimulus amplitude tests the property of homogeneity. The variation in the frequency content of the stimulus tests the property of additivity. The variation in the rotation axis of the stimulus tests the property of spatial superposition.

| Rotation axis | Amplitude (max, °) | Frequency (Hz)       |
|---------------|--------------------|----------------------|
| x, y, z       | 2.5                | 4, 8, 12             |
|               | 5                  | 1, 2, 3, 4, 6, 8, 12 |
|               | 10                 | 2, 4, 8, 12          |
| x, y, z       | 7.7                | 1 + 3                |
|               | 9.8                | 3 + 4                |
|               | 5                  | 1, 2, 3, 4, 6, 8, 12 |

The basic stimulus pattern was a sinusoidal grating with a constant spatial frequency of 0.05 cycle/° (figure 2.2, B). This was oscillated sinusoidally about the six axes x, y, z, x', z' and x'' (these axes are explained and illustrated in the next section). The moths were exposed to two classes of stimuli: single-sine stimuli and double-sine (sum of sines) stimuli. The single-sine stimuli oscillated at frequencies between 1 Hz and 12 Hz, with amplitudes ranging from 2.5° to 10°. The double-sine stimuli combined 1 Hz and 3 Hz, or 3 Hz and 4 Hz oscillations in one single motion and were only presented about the x, y and z-axes. Each double-sine stimulus was generated by adding two individual waveforms of 5° amplitude without relative phase shift (appendix A, figure A.1).

Each stimulus imitates the optic flow a moth would experience during perturbations

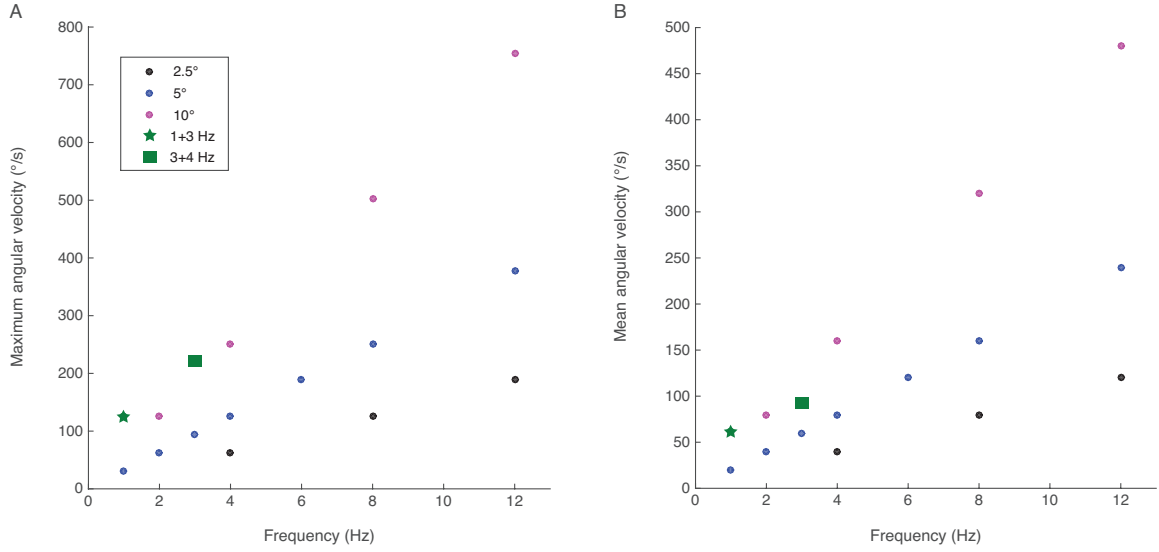


**Figure 2.1:** Angular velocities of the stimuli plotted as a function of frequency and stimulus amplitude (2.5° in black, 5° in blue, 10° in magenta). Graph A shows the maximum angular velocities, and graph B shows the mean angular velocities of the single- and double-sine stimuli that the moths were exposed to in the tethered experiments.

about an equilibrium state of hover. The choice of spatial frequency, oscillation amplitudes and temporal frequencies coincided with those used to evaluate the response optima of wide-field, motion-sensitive interneurons in previous studies [27] [44]. Choosing 1 Hz as the lowest temporal frequency is supported by investigations of abdominal responses in *M. sexta* which suggest that the optomotor system functions as a high-pass filter, with a passband beginning at  $\sim 0.5$  Hz [41]. The visual stimuli were generated so as to ensure a constant contrast frequency at every point within the visual field [45]. This is important because as mentioned in the introduction, the EMDs are sensitive to contrast frequency. Hence, a constant contrast frequency for each point on the sphere meant that every point on the moth's retina would experience the same temporal change in brightness. The moth's head was never fixed. Hence, although I controlled the pattern projected onto the sphere, the moths had some influence on the dynamic range of motion they perceived.

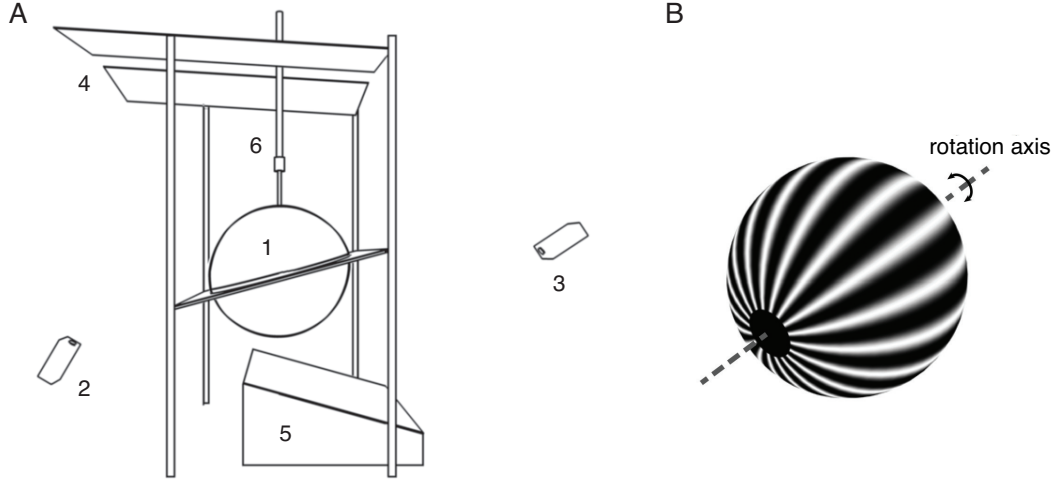


**Figure 2.2:** (A) Diagram of the virtual reality flight simulator. Visual stimuli were projected onto the acrylic sphere (1) via two projectors (2, 3) and a system of mirrors (4, 5), whilst the moth was tethered to a force transducer located at the end of a steel arm (6) in the centre of the sphere. (B) The projected stimuli oscillated in a sinusoidal motion about six different axes so as to simulate multiple types of perturbations.

The images were rendered in 3D modelling software (3ds Max, Autodesk, CA, USA). The images were projected onto the sphere by two synchronised digital projectors which were fitted with DC lamps (LT170, NEC, Japan) and micromirror chipsets (ALP-2, ViALUX, Chemnitz, Germany). The images measured  $1024 \times 768$  pixels and were projected at a rate of 144 Hz with 8 bit greyscale. Two neutral density filters (62 mm HMC NDX2 and NDX4, HOYA, Japan) were screwed onto each projector in order to simulate crepuscular light conditions. Whilst the stimulus was off, the moth was exposed to a static screen that created an overall light intensity of 23 lx, and when the stimulus was projected, the intensity decreased to 10 lx. These light levels correspond to twilight conditions and match the settings used in previous studies with *M. sexta* [41] [46] [28].

## 2.3 Notation of stimulus axis, stimulus and motor responses

In this study, capital letters denote the force and moment responses (output) and lower case letters denote stimuli (input) and stimulus axes. All axes are right-handed, body-fixed axes with their origin in the moth's centre of mass and all axes are fixed with respect to each other. The cardinal axis system consists of the  $x$ ,  $y$ , and  $z$ -axes (figure 2.3).  $x$  is horizontal and  $z$  points vertically down.

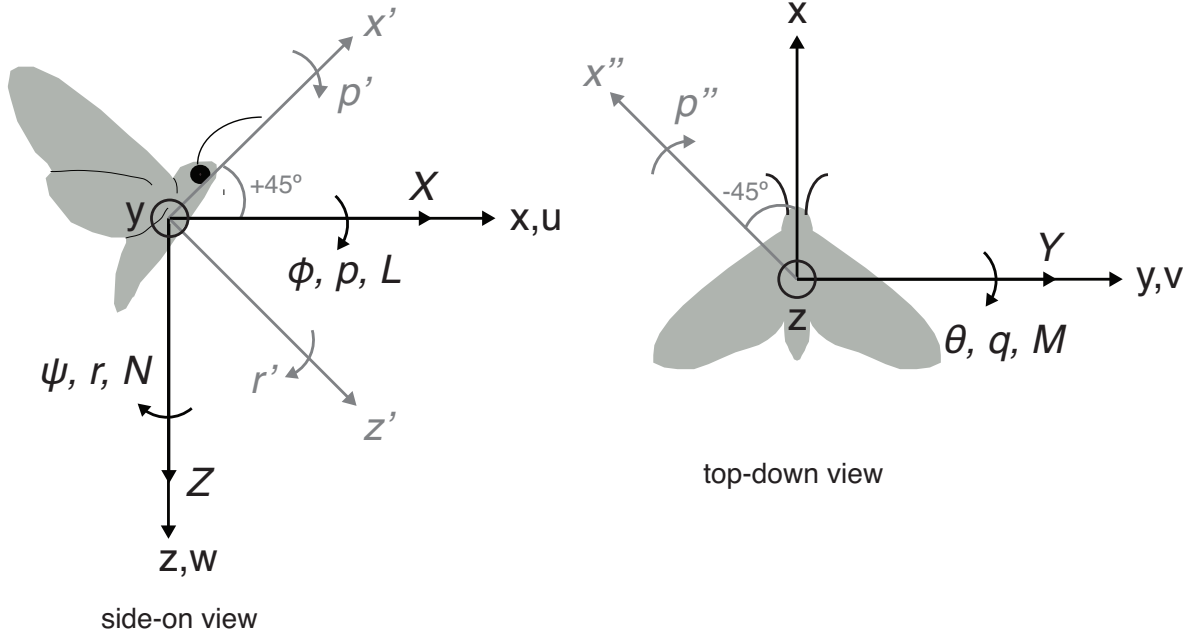


**Figure 2.3:** Graph illustrating the six rotation axes  $x$ ,  $y$ ,  $z$ ,  $x'$ ,  $z'$  and  $x''$ . The corresponding angular rates of the stimuli are  $p$ ,  $q$ ,  $r$ ,  $p'$ ,  $r'$  and  $p''$ .  $\phi$ ,  $\theta$ , and  $\psi$  represent angular roll, pitch, and yaw position of the stimulus. The moth's responses are always resolved about the cardinal  $x$ ,  $y$ , and  $z$ -axis (the cardinal axes are marked in black). The corresponding force responses are  $X$ ,  $Y$ , and  $Z$ . The corresponding moment responses are  $L$ ,  $M$ , and  $N$ . The coordinate system with  $x'$ , and  $z'$  is generated by rotating the cardinal coordinate system  $x$ ,  $y$ , and  $z$  by  $+45^\circ$  around the  $y$ -axis. The coordinate system with  $x''$  is generated by rotating the cardinal coordinate system  $x$ ,  $y$ , and  $z$  by  $-45^\circ$  around the  $z$ -axis.

## Chapter 2 Materials and methods for the tethered experiments

The angular position of the stimulus rotating about the x, y, or z-axis is denoted by  $\phi$ ,  $\theta$ , and  $\psi$ , respectively. The angular rate of the stimulus rotating about the x, y, or z-axis is denoted by  $p$ ,  $q$ , or  $r$ , respectively. The force measured along the x, y, or z-axis is denoted by  $X$ ,  $Y$ , and  $Z$ , respectively. The moment response measured about the x, y, or z-axis is denoted by  $L$ ,  $M$ , and  $N$ , respectively. Symbols with one prime refer to the axis system which is obtained by rotating the cardinal axis system through  $+45^\circ$  about the y-axis of the cardinal system. Hence, the primed axes  $x'$  and  $z'$  approximately coincide with the body principal axes.  $p'$  is the angular rate of the stimulus rotating about  $x'$ , and  $r'$  is the angular rate of the stimulus rotating about  $z'$ . Because of the rotation about the y-axis,  $y'$  is equivalent to  $y$ . Symbols with a double prime refer to the axis system which is obtained by rotating the cardinal axis system through  $-45^\circ$  about the z-axis of the cardinal system. Hence,  $p''$  is the angular rate about the  $x''$ -axis. Because this rotation is made about the z-axis,  $z''$  is equivalent to  $z$  of the cardinal axis system, whilst  $y''$  is simply the reflection of  $x''$  in the insect's plane of symmetry. It follows that there is no need to measure responses to stimuli about  $y''$  separately, because on grounds of symmetry we would expect the insect to produce a mirror symmetric response. Irrespective of the stimulus, the response is always resolved for  $L$ ,  $M$ , and  $N$ , i.e. the moments generated about the x, y, and z-axis, respectively. An on-axis response corresponds to a moment response along the axis of stimulus, and an off-axis response refers to a moment response at  $90^\circ$  to the axis of stimulus. For example, if the moth is exposed to a yaw stimulus (rotation about  $z$ ), then  $N$  is the on-axis response whereas  $L$  is the off-axis response. The moment responses generated in response to a particular stimulus are denoted for example as  $L_\phi$  or  $L_p$ , i.e. a roll moment  $L$  generated in response to a change in roll angle  $\phi$ , or a roll moment  $L$  generated in response to roll rate  $p$ .

## **2.4 Experimental trials and data acquisition**

All moths involved in a given experiment were presented with the same subset of stimuli, but in a different, randomised order. A 2 Hz and 5° amplitude roll stimulus was used to monitor the moth’s performance, and was presented repeatedly throughout the experiment. If the response to this monitoring stimulus had diminished significantly compared to the initial response, the moth was removed from the force transducer, fed with sugar solution and stored in a 12°C fridge over night. The experiment was then resumed the following day. Except for this monitoring stimulus, no pattern was presented more than once to any moth. Each stimulus was presented for about two minutes, allowing for at least one minute of continuous flight recording. The simultaneous forces and moments produced by the moth were measured using a six-component strain gauge balance (Nano17, ATI Industrial Automation, NC, USA) with constant voltage excitation (2210A Signal Conditioning Amplifier, Vishay, NC, USA). The signal was pre-amplified by a factor of 300 and low pass filtered at 1 kHz before being digitised at 10 kHz (PowerLab/16SP, ADInstruments, NSW, Australia) and recorded onto a computer. During the interval of uploading the next stimulus, the moth was exposed to a static screen for roughly one minute. Then, another random visual stimulus was presented. Depending on the fitness of the moth, the duration of the experiment varied between 30 minutes and 1.5 hours.

## **2.5 Data processing**

The voltage recordings were down-sampled to 1 kHz and then transformed into forces and moments by using the previously calculated calibration matrix. This calibration matrix was calculated by measuring the transducer’s output after loading it with clearly defined weights [9]. The weights caused a known force and moment and were adapted to the

## Chapter 2 Materials and methods for the tethered experiments

range of forces and moments produced by the moth. The measured voltage outputs were regressed on the applied forces and moments and inverted in order to acquire a linear calibration matrix. A dynamic calibration was performed whereby the same forces and moments were applied to the transducer but with the addition of a periodic excitation. The dynamic calibration did not reveal any significant dynamic effects. In this study, I set a focus on time delays associated with the sensorimotor transform from visual stimulus to moment response. I therefore need to ensure that the phase of the measured responses is neither affected by resonance properties or motion of the mount, nor by properties of the mount with a moth tethered to it. As communicated by Dr. Shane Windsor, the natural frequency of the mount is 18 Hz when tapped with and without a hawkmoth *Hyles lineata* attached and when the steel arm is extended into the centre of the sphere. I therefore assume that the force transducer does not introduce any phase shifts into the measured moments and hereby does not distort the time delays discussed later on in this study. Although, a more detailed understanding of the dynamic properties of the mount with an attached *Manduca sexta* would be preferential. Before each experiment, a shunt calibration was performed in order to confirm that the transducer's electrical properties had not changed significantly.

After having transformed the voltage measurements into forces and moments they were then resolved at the moth's centre of mass (CoM). The location of the CoM was estimated separately for each individual moth. To do this, I clipped off the wings from the frozen body, and suspended the moth from a pin at various pivot points on the moth's body and appendages (appendix A, figure A.2). I took images of the moth's body next to which I had hung a plumb line to evaluate the alignment of the suspended body relative to gravity. Using MATLAB (MATLAB v. 7.4, The Mathworks Inc., Natick, MA, USA), I identified the intersection of the plumb line and the body axis and aligned and digitally overlaid

## Chapter 2 Materials and methods for the tethered experiments

these images to determine the average location of the CoM in the sagittal plane of each moth. The CoM was evaluated in percentage of body lengths from the head (for  $n=26$ ,  $0.44 \pm 0.01$ , mean  $\pm$  SEM). Side-on photographs were then used to estimate the distance between the force transducer and the CoM (appendix A, figure A.3).

After transferring the measurements to the CoM, all input signals (i.e. visual stimuli) and output signals (i.e. forces and moments) were individually converted into the frequency domain using the chirp z-transform (CZT, also called the zoom-transform). The CZT implements window averaging (Welch's method) across the discrete time signals, using Hanning windows of 8 s duration and 80% overlap. The advantage of the CZT over the fast Fourier transform (FFT) is that it can be used to calculate the frequency spectrum of a signal over an independently specified range of frequencies, rather than at evenly-spaced intervals up to the Nyquist frequency as is the case for the usual FFT [47]. Also, the CZT is applied when the signal of interest is short or truncated. [48]. It is commonly used in frequency domain system identification because of the improved resolution and accuracy that it offers over the FFT by zooming in upon a particular range of frequencies [49]. For every individual trial, the CZT delivers the power spectrum of the stimulus  $P_{xx}$ , the power spectrum of the response  $P_{yy}$  and the cross power spectrum  $P_{xy}$  across a frequency spectrum of 0 to 60 Hz, with a resolution of 0.1 Hz. Using these three variables I then evaluated the frequency response function  $H$  (equation 2.1), the magnitude response (equation 2.2), the phase response (equation 2.3) and the coherence  $\gamma^2$  (equation 2.4). These four values were evaluated for each force and moment response, at the fundamental oscillation frequency of the stimulus. A more detailed description of the data processing is provided in appendix A.2.

$$H = \frac{Pxy}{Pxx} \quad (2.1)$$

$$\text{magnitude} = \sqrt{\text{real}(H)^2 + \text{imag}(H)^2} \quad (2.2)$$

$$\text{phase} = \text{atan}\left(\frac{\text{imag}(H)}{\text{real}(H)}\right) \quad (2.3)$$

$$\gamma^2 = \frac{|Pxy|^2}{Pxx \cdot Pyy} \quad (2.4)$$

The magnitude is the ratio of the system's output and the system's input. In chapter 3, the magnitude is the ratio of the moment response and the angular position of the stimulus, normalised by the moth's mass. In chapter 4 on the other hand, the magnitude is the ratio of the moment response and the angular rate of the stimulus, normalised by the moth's mass. Both approaches are equivalent ways of representing the same behaviour and the choice of the system's input is therefore arbitrary. But I used both approaches to draw out different aspects of the responses in the two corresponding chapters. The phase represents the temporal lead (positive phase value) or lag (negative phase value) of the response relative to the visual stimulus, measured for a particular oscillation frequency. The magnitude and phase values were evaluated for each trial and were then pooled to evaluate arithmetic and circular means respectively. The coherence is a measure of the proportion of the response signal which is linearly attributable to the stimulus. Hence, it is a measure of the power which is linearly transferred from the visual stimulus to the moment response. The coherence is free to vary between 0 and 1 and is considered sufficiently high to interpret a response if the sample coherence reaches a threshold of 0.6 [49]. In this case, the amplitude and timing of the moment response relative to the

stimulus are strongly consistent. Note that for a periodic input signal, high coherence could also be achieved even if the system's response contains periodic non-linearities. Hence, high coherence indicates that a significant amount of stimulus power is linearly represented in the response, but it is not a sufficient condition for linearity [50].

## 2.6 The Akaike Information Criterion

The Akaike Information Criterion (AIC) is a Bayesian approach to model selection and was used in chapter 3 and in chapter 4 to select the best model that parameterises the moment responses as a function of the visual parameters. The AIC value measures the negative log likelihood (goodness of fit) of the model penalised by the total number of model parameters  $k$  and sample size  $n$  (i.e. the degree of freedom). For small sample sizes (i.e. when  $n/k$  is smaller than 40 or approximately 40), the Small Sample Corrected Akaike Information Criterion (AICc) should be used instead. The AICc is calculated according to equation 2.5, where SSE is the error sum of squares. The AICc only has a meaning when compared to that of the competing models, whereby the model with the smallest AICc is the model that performs best for the data provided [51]. The relative likelihood  $L_h$  in equation 2.6 indicates the probability of each model  $j$  to minimise the loss of information.  $L_h$  reaches its maximum value of 1 for the model with the smallest AICc value.

$$AICc = n \cdot \log \left( \frac{SSE}{n} \right) + 2k + \frac{2k(k+1)}{n-k-1} \quad (2.5)$$

$$L_h = e^{\frac{AICc, \min - AICc, j}{2}} \quad (2.6)$$

## *Chapter 2 Materials and methods for the tethered experiments*

In summary, I selected a range of 69 stimuli in order to address and test multiple properties of the optomotor system of the hawkmoth *M. sexta*. I fixed the moth to a six degree of freedom force balance and positioned it in the centre of the virtual reality flight simulator. It was then exposed to an array of apparent body rotations which varied in amplitude, frequency and rotation axis. In the next three chapters I will discuss the optomotor responses which are represented in the frequency domain for the purpose of system identification. I will use the Small Sample Corrected Akaike Information Criterion in order to select the models that best describe the optomotor responses, i.e. the dynamic relationship between the flight behaviour and parameters such as the angular position or the angular velocity of the stimulus. In the last chapter of this thesis, I validate the optomotor responses of tethered specimens with the optomotor responses of free flying moths.

## Chapter 3

# Testing the principles of linearity in the dynamic optomotor responses

In order to identify the role of visual feedback in insect flight control and stabilisation I measure the optomotor response. In this chapter, the optomotor response is defined as the dynamic relationship of the moth's aerodynamic moment response and the angular position of the stimulus. Although the neural and muscular components underlying this behaviour are highly non-linear, a number of studies have characterised vision-based flight behaviour in diurnal species by using the well-studied toolbox of linear control theory. In this chapter I explain the basic principles of linear control theory and analyse to what extent this linear framework is applicable for the identification of the optomotor response, i.e. for the identification of the vision-based flight controller in *M. sexta*.

This chapter is structured as follows: In section 3.1, I describe the theory of linear and time-invariant (LTI) systems, and explain the sets of stimuli I am going to use to assess the linearity of the optomotor system. In section 3.2, I analyse the power spectra and find evidence that the optomotor response can be approximated as a quasi-linear

system. This means that I can characterise the optomotor response by focusing on the response generated at the fundamental frequency of the stimulus. In section 3.4, I use the Small Sample Corrected Akaike Information Criterion (AICc) for model selection. This will show that the salient features of the optomotor response are best predicted by non-linear combinations of visual stimulus parameters. Furthermore, the results of this chapter suggest that the system uses different flight control laws and is driven beyond its working range, depending on the stimulus axis.

### 3.1 Theory of linear and time-invariant systems

A linear system (figure 3.1) has a unique relationship between its input and output signal, i.e. between the stimulus  $\epsilon(t)$  and the response signal  $u(t)$ .

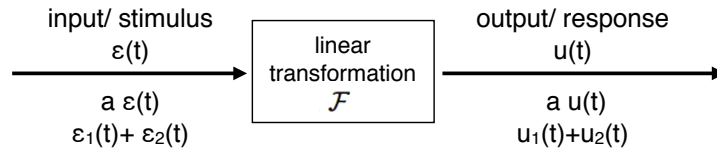


**Figure 3.1:** Schematic of a linear system with its input  $\epsilon(t)$  and output  $u(t)$ . A linear system has to meet the property of homogeneity and the property of additivity. If either one of these two properties is not met, the system is non-linear. Homogeneity is met if a proportional change  $a$  of the input causes the same proportional change in the output. Additivity is met if the sum of the outputs for two individual inputs is equivalent to the output for the sum of inputs.

The system is linear in its input and output if all its input-output pairs obey the property of homogeneity and the property of additivity [52]. Take a system that maps the input to the output with the linear function  $\mathcal{F}$  (equation 3.1, figure 3.1). The property of homogeneity is met if a change in the stimulus by a factor  $a$  causes the same proportional change in the response (equation 3.2). The property of additivity is met if the response

*Chapter 3 Testing the principles of linearity in the dynamic optomotor responses*

to a sum of stimuli  $\epsilon_1(t) + \epsilon_2(t)$  is equivalent to the sum of the individual responses if the system were subject to the two stimuli separately (equation 3.3). Every linear system has the property of homogeneity and the property of additivity. These are necessary and sufficient conditions for a linear transformation. If the system does not meet both properties, the system is non-linear.

$$\mathcal{F}[\epsilon(t)] = u(t) \quad (3.1)$$

$$\mathcal{F}[a\epsilon(t)] = a\mathcal{F}[\epsilon(t)] \quad (3.2)$$

$$\mathcal{F}[\epsilon_1(t) + \epsilon_2(t)] = \mathcal{F}[\epsilon_1(t)] + \mathcal{F}[\epsilon_2(t)] \quad (3.3)$$

If additionally, the system is also constant in time (equation 3.4), the system is considered linear and time-invariant (LTI).

$$\mathcal{F}[\epsilon(t + \delta t)] = u(t + \delta t) \quad (3.4)$$

Homogeneity is tested in section 3.4 by exposing the moth to single-sine stimuli with different stimulus amplitudes. Hence, the oscillation has a constant frequency, but the amplitude changes from  $2.5^\circ$ , to  $5^\circ$  and  $10^\circ$ . The optomotor response has the property of homogeneity if the amplitude of the moment response doubles with a doubling of the oscillation amplitude. Additivity is tested in section 3.5 by exposing the moth to three separate stimuli: two single-sines and one double-sine waveform. The optomotor response is additive if the sum of the responses to both single-sines is equivalent to the response to the double-sine. Hence, I test the moth's ability to distinguish two frequency components from a double-sine waveform. If the optomotor system satisfies these two properties, the linear transfer function  $\mathcal{F}$  describes the full dynamic response behaviour of the system

and can be used to infer the underlying control mechanism.

Before I apply statistical methods to verify homogeneity and additivity, I need to establish whether the moths responded to the stimuli. For this, I analyse the power spectra in section 3.2 and the coherence in section 3.3. The power spectra and the coherence indicate how strongly the response is related to the stimulus. I also use these two parameters to identify the control-relevant moment responses.

## **3.2 Power spectra and time-invariance**

A power spectrum illustrates the power content of a signal across a range of frequencies. The power of a signal at a particular frequency is measured in units of the signal squared per frequency, i.e.  $\text{deg}^2 \text{ s}$  for the stimulus power, and  $\text{N}^2 \text{ mm}^2 \text{ s}$  for the moment response power (more information can be found in appendix A.2). It is a necessary but insufficient condition for linearity that the power in the response signal is only provided at those frequencies present in the stimulus. For instance, if the moth is exposed to a 4 Hz oscillation, we would expect the response power to peak at 4 Hz only. If the response contains power at subharmonic or harmonic frequencies it would indicate non-linearity. Unsurprisingly, there is a large peak at wingbeat frequency ( $23.4 \pm 2.5 \text{ Hz}$ , mean  $\pm$  SD) in the spectra of the moment responses. This power peak is unrelated to the stimulus and indicates the power generated to maintain flight. The power used to maintain flight is  $\sim 20'000$  to  $30'000 \text{ mN}^2 \text{ mm}^2 \text{ s}$ , whereas the power which is used to control and stabilise flight at the stimulus frequencies lies within the range of 0 to  $\sim 5'000 \text{ mN}^2 \text{ mm}^2 \text{ s}$ .

First, I analyse the power spectra for the single-sine stimuli, comprising of oscillation amplitudes of  $2.5^\circ$ ,  $5^\circ$  and  $10^\circ$ , and temporal frequencies of 1 Hz to 12 Hz (a subset of the spectra for single-sine stimuli of  $5^\circ$  amplitude are shown in figures B.1, B.2, and

B.3). For these, most of the response power at frequencies below the wingbeat frequency is concentrated at the fundamental frequency of the stimulus. As shown in figure 3.2, this even holds for the fastest stimuli that I presented (e.g. for a stimulus with a 12 Hz oscillation and  $10^\circ$  amplitude). There is appreciable harmonic content for pitch stimuli provided at 8 Hz and an amplitude of  $10^\circ$ , but the power at the first harmonic of 16 Hz is still less than a third of the power at the fundamental stimulus frequency (figure 3.2, D). Nonetheless, this harmonic response suggests that the quasi-linear assumption loses validity for stimuli of high amplitude and frequency. I cannot identify how much harmonic content is present in the responses to stimuli provided at 12 Hz, because the power contained at wingbeat frequency completely overwhelms the response at this frequency. The power at 1 Hz which is generated in response to roll stimuli of 8 and 12 Hz may be caused by increased abdominal motion.

Second, I analyse the power spectra for the stimuli that I am using to test the principle of additivity. Hence, I compare the power spectra of two double-sine stimuli (1+3 Hz or 3+4 Hz) with the power spectra for single-sine stimuli presented at the same frequencies (1, 3, and 4 Hz). Figure 3.3 shows that in terms of frequency and power, the two discrete power peaks measured in response to the double-sine stimuli (in green) approximately overlap the responses to single-sine stimuli (in red and blue). No power is found at (sub-)harmonic frequencies of the stimulus frequency, except for the aforementioned power peak at the wingbeat frequency. Similar to what is observed in figure 3.2 B, the power at  $\sim 0.5$  Hz may indicate abdominal motion, because potential effects of the DC power should have been eliminated by detrending the measurement signals. As communicated by Prof. Tom Daniel, a consistent subharmonic response behaviour could be detected by applying a coherence analysis across the responses of multiple individuals for a given stimulus.

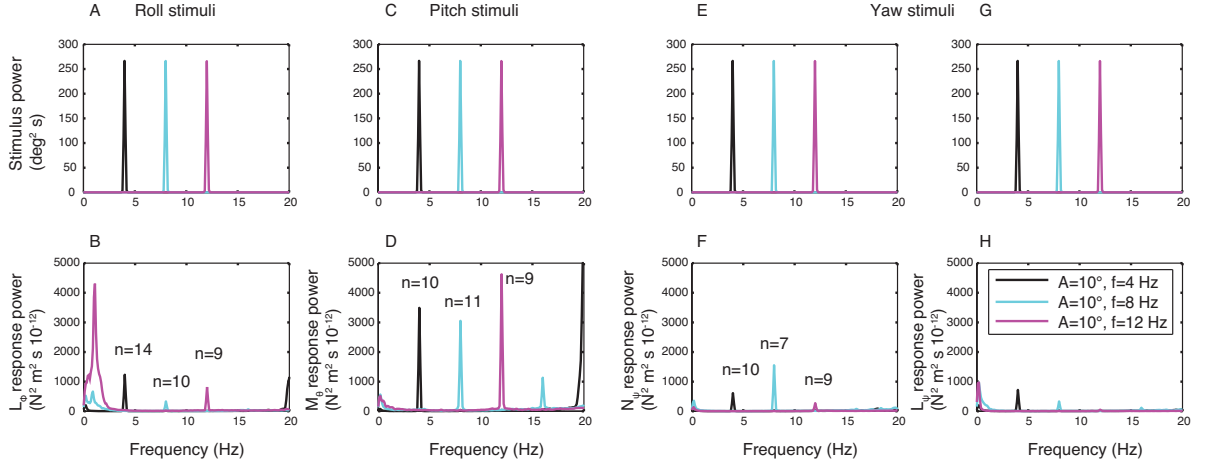


**Figure 3.2:** Subset of the mean power spectra for single-sine stimuli with a  $10^\circ$  stimulus amplitude and frequencies of 4 Hz (black), 8 Hz (blue) and 12 Hz (magenta). The top row shows the stimulus power for roll (A), pitch (C), and yaw (E, G) stimuli. The bottom row shows the on-axis response power to roll (B), pitch (D), and yaw stimuli (E) as well as the off-axis response power to yaw stimuli (H).  $n$  indicates the total number of trials for a particular stimulus and is equivalent to the number of response spectra averaged. These data illustrate the moths' response behaviour for peak angular velocities of 377, 502 and  $754^\circ/\text{s}$ . These responses are plotted across a frequency spectrum of 0 to 20 Hz on a linear scale. The harmonic response to the 8 Hz pitch perturbation (which corresponds to  $\sim 30\%$  of the power at the fundamental frequency) suggests that the quasi-linear assumption loses validity for stimuli of high amplitude and frequency. The peak at 1 Hz which is generated in response to roll stimuli of 8 and 12 Hz may be caused by increased abdominal motion.

From the power spectra I conclude that the moths show strong behavioural responses to the single- and double-sine stimuli. Below the wingbeat frequency of  $\sim 23$  Hz, the moths generate significant response power only at the fundamental frequencies of the stimulus. Hence, the significant behaviour is captured when this system is approximated as a quasi-linear system. I will therefore evaluate the principle of homogeneity and additivity based on the responses generated at the frequencies of the stimulus only.

I investigated the time-invariance of the total force and total moment responses for each trial by calculating the ratio of the mean response in the first half of the down-sampled,

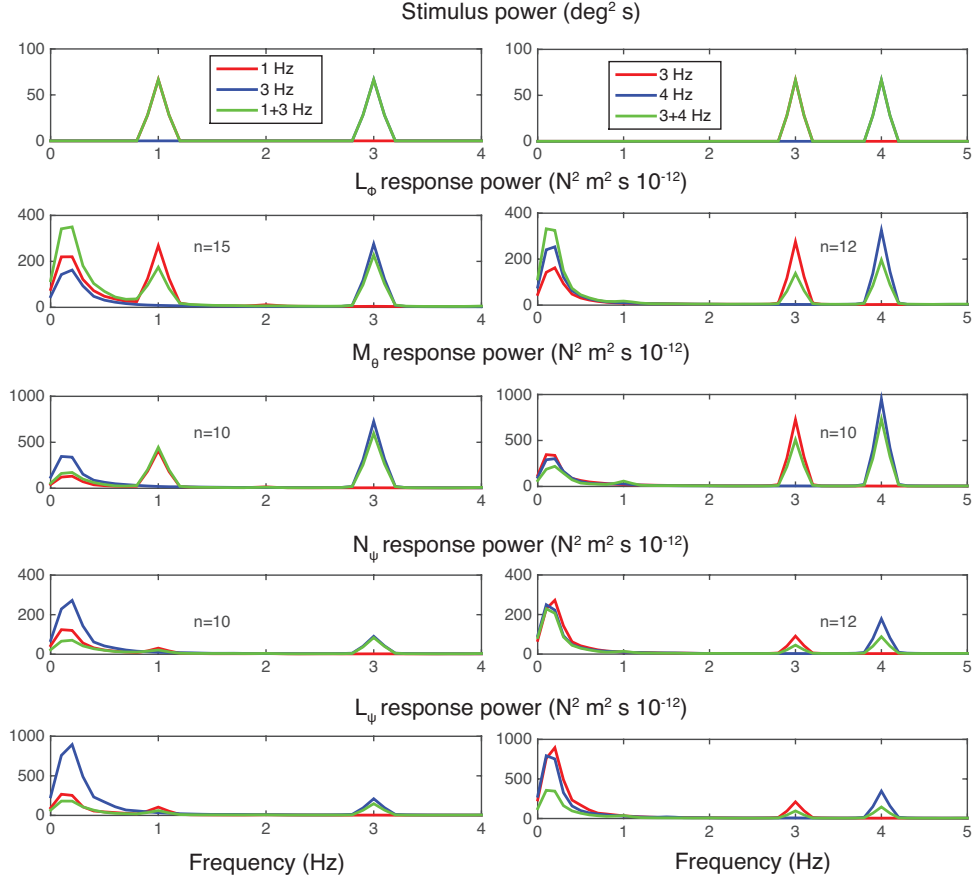


**Figure 3.3:** Mean power spectra for the stimuli used to test the principle of additivity. The rows illustrate 1) the input power spectra, 2) the output spectra for the roll moment response to roll stimuli, 3) the output spectra for the pitch moment response to pitch stimuli, 4) the output spectra for the yaw moment response to yaw stimuli, and 5) the output spectra for the roll moment response to yaw stimuli. Each graph contains three spectra: The left column shows data for the 1 Hz (red), 3 Hz (blue) and 1+3 Hz (green) oscillations; the right column shows data for the 3 Hz (red), 4 Hz (blue) and 3+4 Hz (green) oscillations.  $n$  indicates the total number of trials for the double-sine stimuli and is equivalent to the number of response spectra averaged to get the green line. The response spectra to double-sine stimuli match closely to the sum of the response spectra to single-sine stimuli. Hence, the moths responded to the two frequency components of the double-sine stimuli. There is no significant (sub-)harmonic response power and the power below 0.5 Hz could be caused by abdominal motion.

lowpass filtered and detrended response signal ( $\sim 35$  s) to that of the second half of the response signal. For 358 trials, the mean ratio for the total force is  $1 \pm 0.19$  (mean  $\pm$  SD), and that of the total moment is  $1.03 \pm 0.19$ . Hence, there is no evidence for any systematic tendency for the response to increase or decrease through the trial and I will therefore treat the system as time-invariant.

### **3.3 Selection of the control-relevant response moments with the coherence**

As explained in section 2.5, the coherence indicates how much of the stimulus power is linearly transferred to the response. The coherence is high, i.e. the response is interpretable, if the coherence exceeds 0.6 [49]. The coherence would be low if the response amplitude is inconsistent or if the frequency content of the response is not linearly related to the stimulus. I use the coherence graphs in figures B.1, B.2 and B.3 to select the response moments generated in response to roll, pitch, and yaw stimuli that have high coherence. In other words, I use high coherence as an indicator of moment responses that are relevant to flight control and stability. In response to roll stimuli, the moths generate a large roll moment together with a smaller yaw moment. The pitch moments measured in response to roll have low coherence ( $< 0.6$ ) and are therefore not attributable to the roll stimuli. When I consider the coherence for all 16 roll stimuli used in this chapter, the on-axis response (i.e. the roll moment) has a high total mean coherence ( $\geq 0.6$ ) for all 16 stimuli whereas the off-axis response (i.e. the yaw moment) only has a high total mean coherence for 9 out of 16 stimuli. Hence, I choose to ignore the off-axis responses to roll stimuli for the remainder of this chapter. In response to pitch perturbations, the moths generate a strong and consistent pitch moment response. For pitch stimuli, the off-axis moments

(i.e. the roll and yaw moments) have low coherence and are not attributable to the pitch stimuli. In response to yaw stimuli, the moths generate a strong and consistent yaw moment response together with a comparably strong and consistent roll moment response. The accompanying pitch moments have low coherence and are not attributed to the yaw stimuli. Now that I have identified the control-relevant moment responses, I will focus on these to analyse the principle of homogeneity and the principle of additivity. Figure 3.4 shows the total mean coherence and the number of trials for the control-relevant moment responses generated for single-sine roll, pitch and yaw stimuli. Hence, figure 3.4 shows the moment responses and the number of trials I will use to assess the property of homogeneity of the optomotor system.

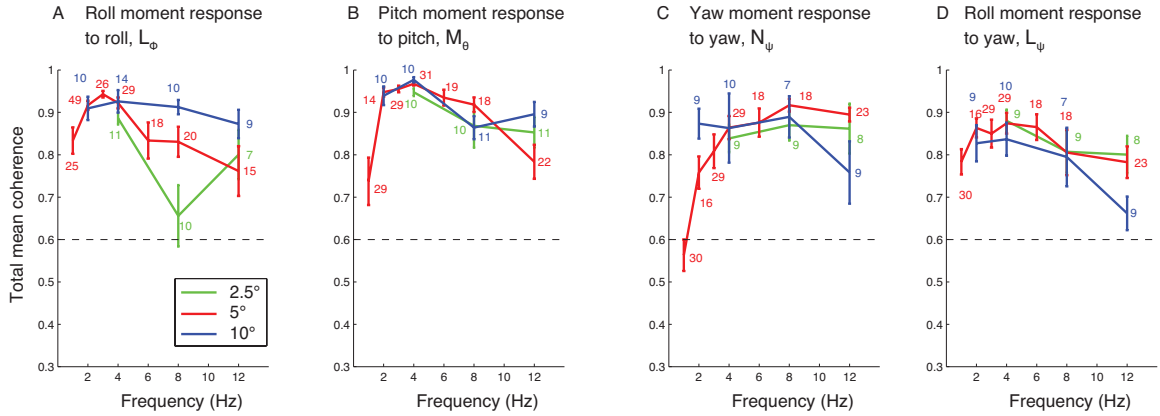


**Figure 3.4:** Total mean coherence for all single-sine stimuli with frequencies from 1 Hz to 12 Hz. These graphs illustrate the total mean coherence for the control-relevant moment responses only. The graphs show the total mean coherence for the roll moment response to roll (A), for the pitch moment response to pitch (B), for the yaw moment response to yaw (C), and for the roll moment response to yaw (D) stimuli. The colours indicate a stimulus amplitude of 2.5° (green), 5° (red) and 10° (blue). The numbers in each graph indicate the total number of trials for a particular stimulus and is equivalent to the number of coherence values averaged. Each data point indicates the mean  $\pm$  SEM.

Figure 3.5 shows the total mean coherence and the number of trials for the control-

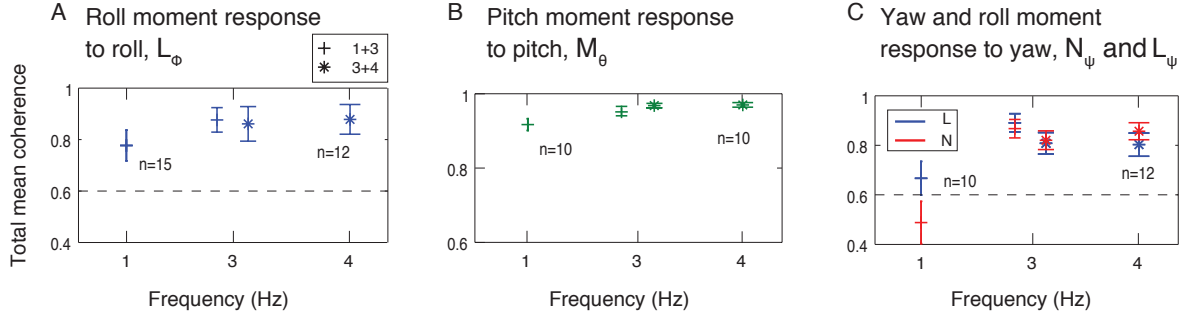


**Figure 3.5:** Total mean coherence for all double-sine stimuli with frequencies of 1+3 Hz (+) and 3+4 Hz (\*). These graphs illustrate the total mean coherence for the control-relevant moment responses only. The graphs show the total mean coherence for the moment responses to roll (A), pitch (B), and yaw (C) stimuli. The colours indicate the roll (blue), pitch (green) and yaw (red) response moment.  $n$  indicates the total number of trials for a 1+3 Hz stimulus (on the left) or a 3+4 Hz stimulus (on the right). Each data point indicates the mean  $\pm$  SEM.

relevant moment responses generated for double-sine roll, pitch and yaw stimuli. Hence, figure 3.5 shows the moment responses and the number of trials of the double-sine stimuli which I will use to assess the property of additivity of the optomotor system.

### 3.4 Testing the principle of homogeneity in the optomotor responses

In order to test whether the optomotor system has the property of homogeneity, I exposed the moths to stimuli presented in table 3.1.

I doubled the stimulus amplitude from  $2.5^\circ$  to  $5^\circ$  and to  $10^\circ$  for single-sine stimuli with a frequency of either 4 Hz, 8 Hz or 12 Hz. At the frequency of 2 Hz I only presented stimuli with a  $5^\circ$  and  $10^\circ$  amplitude. The significant variable is the stimulus amplitude. The optomotor system would meet the property of homogeneity if a doubling of the oscillation amplitude leads to a doubling of the system's moment response. This is equivalent to the

**Table 3.1:** A total of 42 visual stimuli were presented to the moths to test the principle of homogeneity. The single-sine stimuli varied in frequency, in amplitude, and in rotation axis.

| Rotation axis | Amplitude (max, °) | Frequency (Hz)       |
|---------------|--------------------|----------------------|
| x, y, z       | 2.5                | 4, 8, 12             |
|               | 5                  | 1, 2, 3, 4, 6, 8, 12 |
|               | 10                 | 2, 4, 8, 12          |

magnitude and the phase response being independent of oscillation amplitude for a given frequency. The magnitude and phase responses for all stimuli presented in table 3.1 are illustrated in figure 3.6. It becomes clear in figure 3.6 that there is a consistent effect of stimulus amplitude on the measured magnitude and phase responses.

The non-linearity is demonstrated by the fact that larger oscillation amplitudes lead to smaller magnitude responses, especially above a temporal frequency of 4 Hz. All magnitude responses represent that trend, whereby the magnitude responses to a 2.5°, 5° and 10° oscillation amplitude are statistically different from each other only in the case of yaw perturbations. Larger oscillation amplitudes also lead to a shallower roll-off in the phase response, especially above a temporal frequency of 4 Hz. In all phase responses, the phase to a 10° amplitude is significantly smaller than the phase decay for a 2.5° and 5° amplitude. For all types of rotational patterns, the phase responses for a 2.5° and 5° stimulus amplitude are statistically not distinguishable. I therefore conclude that the optomotor system does not have the linear property of homogeneity over the range of stimulus frequencies and amplitudes that I presented.

To test formally for an effect of stimulus amplitude, I compared the performance of 16 competing models fitting either the magnitude or the phase response as a function of amplitude, frequency and their interactions. Equations 3.5 and 3.6 show the global models which describe either the magnitude or the phase response as a function of moth

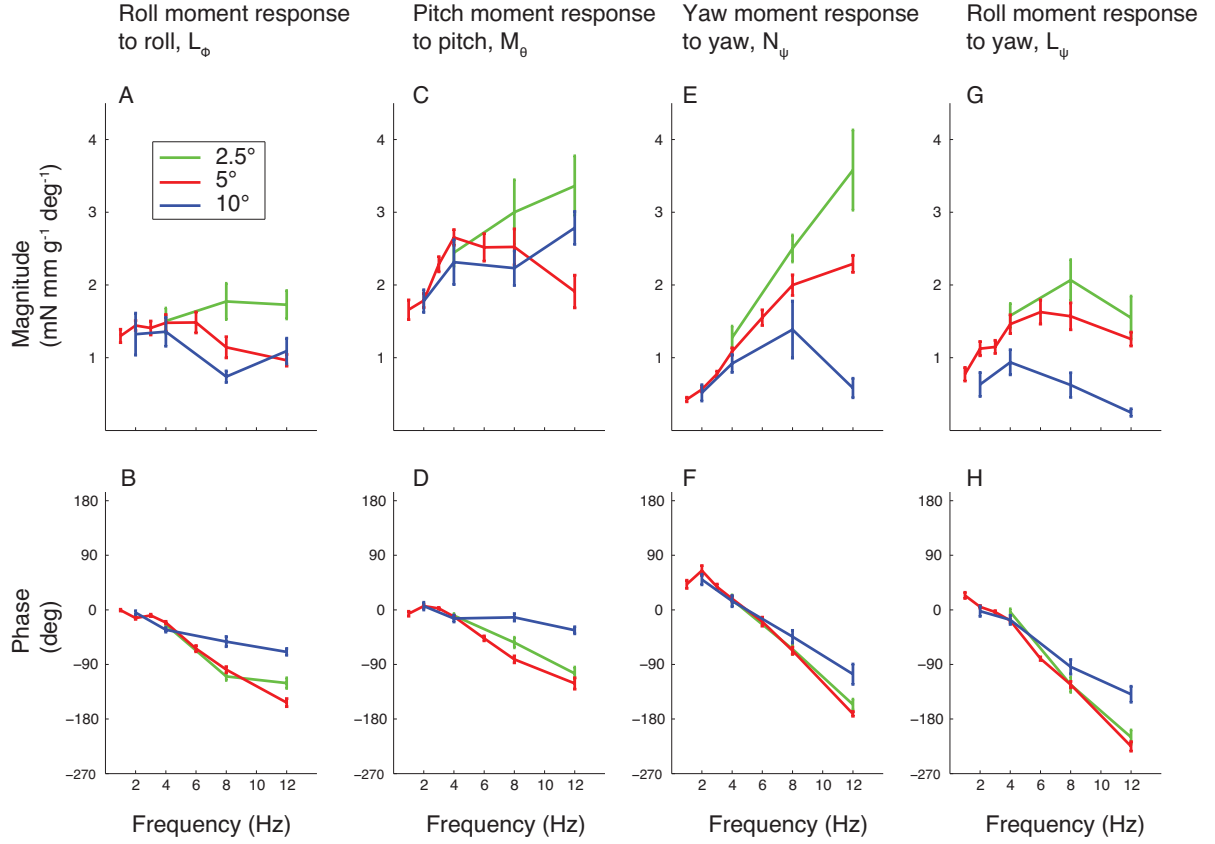


**Figure 3.6:** Measured magnitude responses (top row) and phase responses (bottom row) for single-sine stimuli. The data are plotted on a linear scale for frequencies ranging from 1 to 12 Hz and show the means of the individual means  $\pm$  SEM. The colours indicate the responses to a stimulus amplitude of 2.5° (green), 5° (red) and 10° (blue). The columns show the on-axis responses to roll (A-B), to pitch (C-D), and to yaw (E-F) stimuli. The last column shows the off-axis responses to yaw stimuli (G-H).

identity  $\alpha_i$ , stimulus amplitude  $A$ , frequency  $f$  and combinations thereof. A set of 16 competing models was derived from these full models by alternately setting parameter values  $\beta_i$  to zero. By including  $\alpha_i$  all models accounted for the variation in the mean of the magnitude and the phase responses among individuals. Each competing model represents an ANOVA, with Type I sum of squares, and with the moth identity as a fixed factor, and the amplitude, frequency, and combinations thereof as covariate factors.

$$\text{Magnitude} = \alpha_i + \beta_1 \cdot A + \beta_2 \cdot f + \beta_3 \cdot Af + \beta_4 \cdot f^2 + \beta_5 \cdot Af^2 \quad (3.5)$$

$$\text{Phase} = \alpha_i + \beta_6 \cdot A + \beta_7 \cdot f + \beta_8 \cdot Af + \beta_9 \cdot f^2 + \beta_{10} \cdot Af^2 \quad (3.6)$$

These models were fitted to the eight datasets shown in the eight graphs of figure 3.6. Hence, these models were fitted to the datasets comprising the on-axis magnitude and phase responses to roll, pitch and yaw stimuli and to the off-axis magnitude and phase responses to yaw stimuli. The models were fitted to the responses provided across the whole range of stimuli because all responses had a coherence of  $\geq 0.6$ .

The performance of each competing model is quantified using the Small Sample Corrected Akaike Information Criterion (AICc, section 2.6). This model selection process is based on the likelihood function and penalises competing models in terms of their sample size  $n$  and the number of predictors  $k$ . The complete analysis is provided in appendix B.2. The models that performed best in explaining the magnitude responses are shown in table 3.2. The models that performed best in explaining the phase responses are shown in table 3.3. In all eight models shown in table 3.2 and 3.3, the stimulus amplitude  $A$  is either present as a main effect or has an effect in interaction with the frequency  $f$  or the frequency squared. I therefore conclude that the optomotor system does not meet the property of homogeneity.

Figure 3.7 shows these eight functions plotted over the range of stimulus amplitudes and frequencies used in the experiments. Hence, these surface plots illustrate the best estimate of the moths' response behaviour presented in figure 3.6. These surface plots may be considered as graphical representations of describing functions. A describing function is a technical term used in non-linear systems analysis to approximate systems

**Table 3.2:** The four empirically derived functions shown below describe the magnitude response to roll, pitch and yaw. They have been individually selected from a family of 16 competing models. Their performance has been evaluated using the AICc. All models account for the variation in mean magnitude among individuals  $\alpha_i$  and for the variation explained by the stimulus amplitude  $A$ , the frequency  $f$  or non-linear combinations thereof.

Magnitude response:

---


$$L_\phi = \alpha_i - 0.006 \cdot Af$$

$$M_\theta = \alpha_i - 0.06 \cdot A + 0.30 \cdot f - 0.02 \cdot f^2$$

$$N_\psi = \alpha_i - 0.003 \cdot A + 0.37 \cdot f - 0.003 \cdot Af^2$$

$$L_\psi = \alpha_i - 0.04 \cdot A + 0.36 \cdot f - 0.01 \cdot Af - 0.02 \cdot f^2$$

**Table 3.3:** The four empirically derived functions shown below describe the phase response to roll, pitch and yaw. They have been individually selected from a family of 16 competing models. Their performance has been evaluated using the AICc. All models account for the variation in mean phase among individuals  $\alpha_i$  and for the variation explained by the stimulus amplitude  $A$ , the frequency  $f$  or non-linear combinations thereof.

Phase response:

---


$$L_\phi = \alpha_i - 3.85 \cdot A - 18.95 \cdot f + 1.18 \cdot Af$$

$$M_\theta = \alpha_i + 0.39 \cdot A + 0.59 \cdot Af - 0.96 \cdot f^2$$

$$N_\psi = \alpha_i - 3.25 \cdot A - 16.16 \cdot f + 0.84 \cdot Af - 0.68 \cdot f^2$$

$$L_\psi = \alpha_i - 11.06 \cdot A - 30.98 \cdot f + 2.56 \cdot Af - 0.06 \cdot Af^2$$

whose output depend on the frequency as well as the amplitude of the input [53]. The describing function also models the output at the input frequency under the assumption of quasi-linearity.

Figure 3.7 shows that the describing functions faithfully reproduce the salient features of

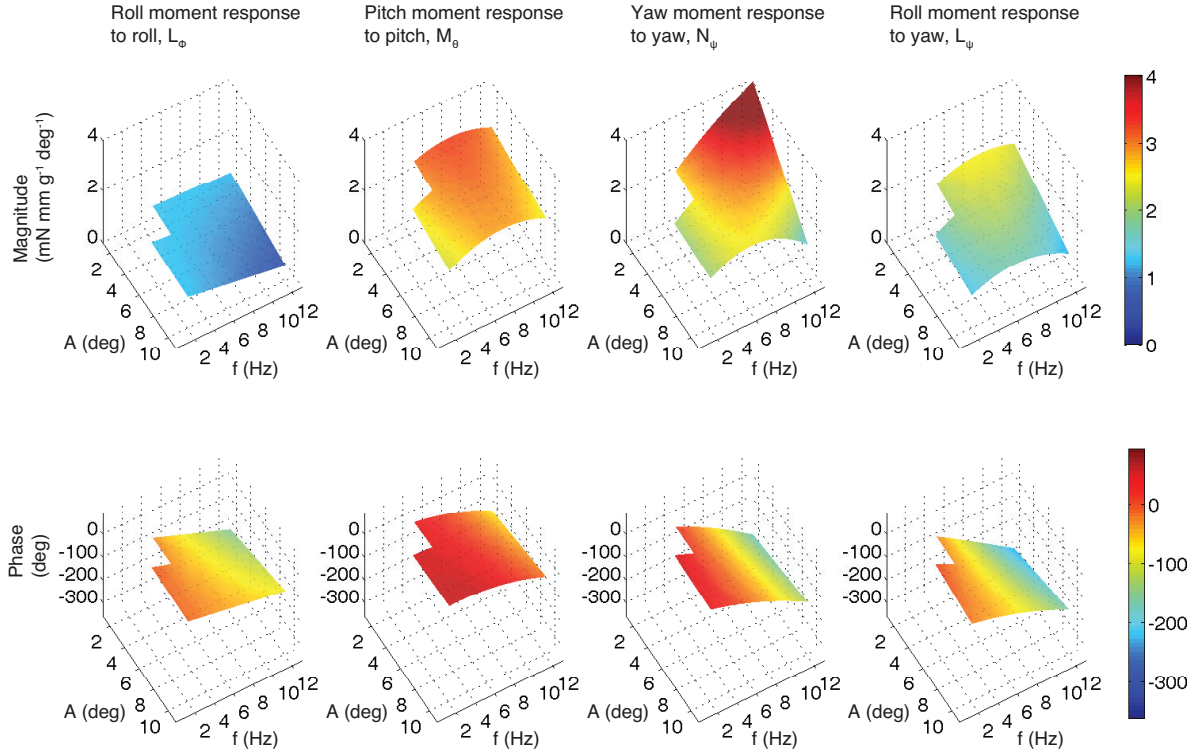


**Figure 3.7:** Graphical representation of the describing functions for the magnitude (top row) and phase (bottom row) responses to single-sine stimuli, plotted on a linear scale with stimulus amplitude  $A$  and frequency  $f$ . The columns represent the predicted on-axis magnitude and phase responses for 1) roll, 2) pitch and 3) yaw perturbations. Column 4) illustrates to the predicted off-axis roll moment response to yaw perturbations. The colour coding indicates the magnitude and phase values and is consistent across a row. This set of functions faithfully reproduce the salient and non-linear features of the optomotor response and are therefore useful for understanding mechanisms underlying the behaviour.

the measured responses and are the best estimate of how the optomotor system responds to changes in stimulus amplitude and frequency. Hence, they not only act as a lookup table for the moment responses, but also help us understand the non-linear relationship between stimulus parameters and the measured moments. They provide evidence for the variation in response behaviour as a function of the rotation axis, and they provide evidence that

the moment responses do not double with the stimulus amplitude, especially not in the case of yaw stimuli. Subsequently, the important question is whether this non-linear effect of amplitude causes the optomotor system to behave non-linearly within its useful working range. Whilst it is easier to quantify homogeneity by using the magnitude and phase responses, the change in the moment responses provide a more intuitive indication of the system's working range, which I define as the range of stimulus amplitudes and frequencies across which there is no decline in the moment response. This is because the response to apparent motion should be unambiguous over the range of velocities that the visual system must discriminate. The normalised moment responses (normalised by the moth's mass) generated in response to roll, pitch and yaw stimuli are shown in figure 3.8, which is a key figure in this thesis. The main observation in figure 3.8 is that for a given angular velocity of the stimulus, the moment responses to roll and pitch stimuli vary with stimulus amplitude and frequency, whereas the moment responses to yaw stimuli collapse onto one curve. In response to yaw stimuli, the on-axis and off-axis moments increase monotonically with angular velocity until they reach a velocity optimum ( $\sim 320^\circ/s$  for the on-axis response and  $\sim 160^\circ/s$  for the off-axis response). For image velocities exceeding this optimum, the response drops and is ambiguous. This drop in the moment responses to yaw stimuli indicates a non-linearity. Or it indicates that the system has reached the limit of its useful working range, i.e. it is being exposed to angular velocities that exceed the value it can usefully interpret. The two moment response curves in figure 3.8,C and 3.8,D strongly resemble the velocity tuning curve of an EMD (figure 1.2), or the response curve of a fly's wide-field directionally-selective HS-cell [1] [54] [55]. An HS-cell integrates signals from EMDs located along the equator of the visual field of view and therefore encodes horizontal optic flow. The responses of *M. sexta* to yaw stimuli are likely to be driven by cells similar to HS-cells. Shoemaker et al. [56] showed that HS-cells of the

hoverfly *Eristalis tenax* maintains this characteristic response curve for yaw rotations of panoramic natural imagery. This suggests that response to yaw stimuli are quite robust to variations in the spatial texture of the scenery.

All moment responses plotted in figure 3.8 have a coherence  $\geq 0.6$ , hereby suggesting that the whole range of stimulus parameters is being perceived and responded to with a significant amount of power that is linearly attributable to the stimulus. Potentially, another sensory modality could provide rate damping due to a fast feedback, which then brings the optomotor system back into a useful operating range for yaw stimuli. This could explain why the coherence is still  $\geq 0.6$ . I conclude from figure 3.8 that the system operates with different control strategies depending on the rotation axis of the stimulus. Because the responses reflect a sensitivity to the stimulus amplitude, there seems to be an adaptation mechanism operating when the moth is exposed to roll and pitch stimuli. Whereas for yaw stimuli, there is no clear sensitivity to amplitude and hence, for the control of yaw stimuli there appears to be no such adaptation mechanism.

I conclude that there is a non-linear effect of stimulus amplitude within the optomotor system's useful working range in response to roll and pitch stimuli. And the non-linear effects of amplitude arise at the limit or outside the system's useful working range in response to yaw stimuli.

### **3.5 Testing the principle of additivity in the optomotor responses**

The principle of additivity is tested by comparing the moth's response behaviour to three separate stimuli, i.e. to two single-sines and to one double-sine waveform. The optomotor response is additive if the sum of the responses to both single-sine stimuli is equivalent to

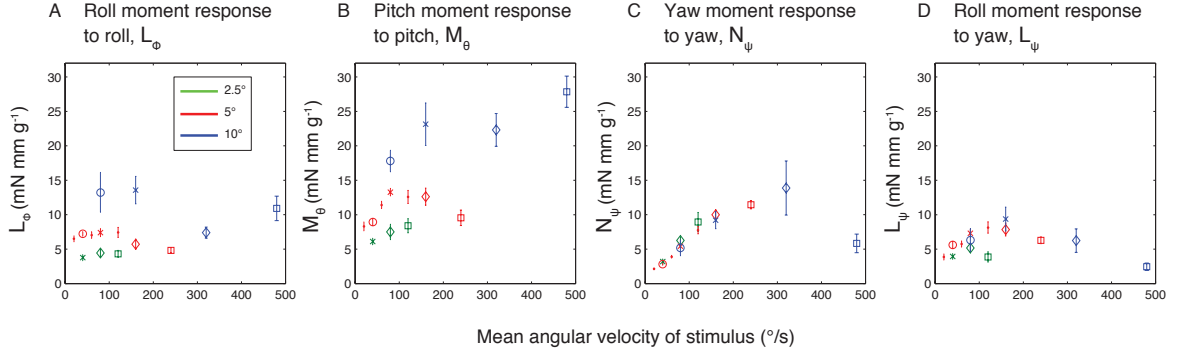


**Figure 3.8:** The normalised moment responses to single-sine stimuli plotted against the mean angular velocity of the stimulus. The colours indicate the stimulus amplitude of  $2.5^\circ$  (green),  $5^\circ$  (red) and  $10^\circ$  (blue). The symbols indicate the temporal frequency of 2 Hz (o), 4 Hz (x), 8 Hz ( $\diamond$ ), and 12 Hz ( $\square$ ). The on-axis moment responses to yaw collapse onto one line which increases monotonously to an angular velocity of  $\sim 320^\circ/\text{s}$ , above which the output is ambiguous. This behavioural trend matches the behaviour of correlation-type elementary motion detectors. In contrast to the responses to yaw perturbation, the responses to roll and pitch do not seem proportional to angular velocity and instead seem to be more sensitive to stimulus amplitude.

the response to the double-sine stimulus. This is equivalent to saying that the response to a particular frequency should be independent of whether the frequency appeared in a single- or double-sine stimulus, if the system is additive. To test this, I exposed each moth to three single-sine stimuli with frequencies of 1, 3, and 4 Hz; and to two double-sine stimuli with a frequency content of 1+3 Hz, and 3+4 Hz (see table 3.4).

**Table 3.4:** A total of 15 stimuli were presented to the moths to test the property of additivity of the optomotor system. The two double-sine and three single-sine oscillations were presented as roll, pitch and yaw stimuli.

| Rotation axis | Amplitude (max, $^\circ$ ) | Frequency (Hz) |
|---------------|----------------------------|----------------|
| x, y, z       | 5                          | 1, 3, 4        |
|               | 7.7                        | 1 + 3          |
|               | 9.8                        | 3 + 4          |

The mean angular velocities used to investigate the principle of additivity lie below

160°/s (figure 2.1) and therefore, following the observations from figure 3.8, any behavioural responses should occur within the system's useful working range.

The magnitude and phase responses for the additivity tests are plotted in figure 3.9.

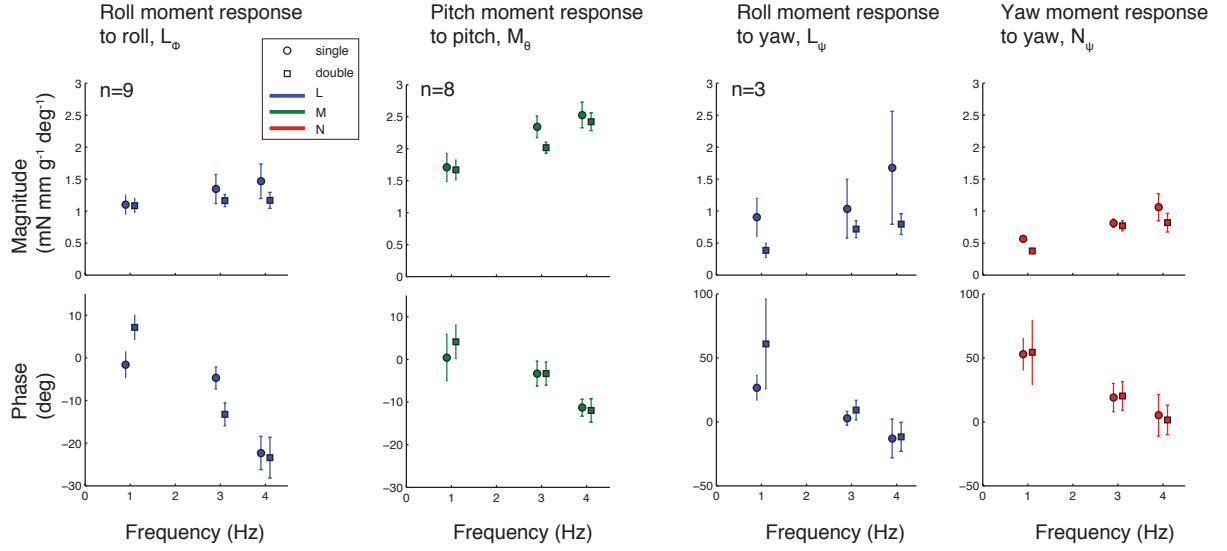


**Figure 3.9:** Magnitude and phase responses to roll, pitch and yaw stimuli used to test the property of additivity. Each point indicates the mean of the individual means  $\pm$  SEM for a frequency presented in a single-sine (o) or double-sine ( $\square$ ) motion. The colours indicate the roll (blue), pitch (green), and yaw (red) response moments.  $n$  indicates the number of trials averaged per data point. Each moth was exposed to five stimuli in total: single-sine stimuli of 1, 3, and 4 Hz and double-sine stimuli of 1+3 Hz and 3+4 Hz. Each trial included in the mean value had a coherence  $\geq 0.6$ .

The magnitude and the phase responses of this balanced experimental design were tested separately with a ANOVA models, with the moth identity as a random factor and the frequency and the setup as fixed factors. The setup defines whether the response was given to a frequency that was presented in a single-sine or in a double-sine oscillation. Because I chose the Type I sum of squares, the models indicated whether there was an effect of setup after accounting for the moth identity and the frequency. Based on the finding of amplitude-dependent non-linearities in the previous section, it is unsurprising

that there is statistical evidence for a difference in some of the magnitude responses, according to whether the stimulus was presented as a single- or double-sine (table 3.5). Nevertheless, it is clear from figure 3.9 that the size of any effect is small.

**Table 3.5:** Results of ANOVA tests, controlling for moth identity, frequency, and setup. The setup indicates whether the frequency was presented in a single-sine or in a double-sine motion.  $B_{single}$  is the parameter estimate (effect size) for the response to a single-sine stimulus. It is given in the units of the magnitude or phase, respectively, and is defined relative to the parameter estimate  $B_{double}=0$  for the responses to the double-sine stimuli. The values in parentheses are the lower and upper limit of the 95% confidence interval. The shaded values indicate that the roll magnitude response to single-sine oscillations of roll and yaw stimuli is statistically different from the roll magnitude response to double-sine stimuli, but only with a small effect size.

|                           | Magnitude                          | Phase                                 |
|---------------------------|------------------------------------|---------------------------------------|
| on-axis response to roll  | $F_{1,51} = 5.274$                 | $F_{1,51} = 0.285$                    |
|                           | $p = 0.026$                        | $p = 0.596$                           |
|                           | $B_{single}=0.195$ (0.025, 0.365)  | $B_{single}=1.358$ (-3.749, 6.465)    |
| on-axis response to pitch | $F_{1,45} = 3.207$                 | $F_{1,45} = 0.194$                    |
|                           | $p = 0.080$                        | $p = 0.662$                           |
|                           | $B_{single}=0.174$ (-0.022, 0.370) | $B_{single}=-0.906$ (-5.045, 3.234)   |
| on-axis response to yaw   | $F_{1,15} = 3.090$                 | $F_{1,15} = 0.001$                    |
|                           | $p = 0.099$                        | $p = 0.980$                           |
|                           | $B_{single}=0.145$ (-0.031, 0.321) | $B_{single}=0.156$ (-13.147, 13.458)  |
| off-axis response to yaw  | $F_{1,15} = 7.159$                 | $F_{1,15} = 2.044$                    |
|                           | $p = 0.017$                        | $p = 0.173$                           |
|                           | $B_{single}=0.546$ (0.111, 0.982)  | $B_{single}=-13.229$ (-32.951, 6.494) |

The parameters  $B_{single}$  in table 3.5 are given in the units of the magnitude (mN mm  $g^{-1}$   $deg^{-1}$ ) or phase (deg), respectively. In general, the magnitude was higher in response to single-sine stimuli, when compared to the magnitude response to double-sine stimuli. The natural way to test for differences in phase is to use circular statistics, but these are not well suited to the experimental design I used because of the need to account for moth identity, frequency and setup. Because the phase values remain in a narrow range the use of circular statistics is unnecessary, and I applied the same linear statistics to test for

differences between the phase responses to single- and double-sine stimuli. There is no significant difference in phase between stimuli presented as single- or double-sines (table 3.5).

In summary, presenting stimuli of different frequencies in combination with each other diminished their magnitude response, but only to a small extent, and did not significantly affect the phase of the response. Although there is evidence for a difference between the magnitude response to a single-sine and double-sine roll and yaw stimuli, the effect size is small and the system can be approximated as having the property of additivity in respect of the particular double-sine stimuli that were presented.

### **3.6 Estimation of the controller's time delay from the phase responses**

For all roll, pitch and yaw stimuli, the moths generate moment responses of the appropriate sense to counteract their apparent self-motion (i.e. to compensate for motion blur), at least when the on-axis phase of the response is between  $-90^\circ$  and  $+90^\circ$  (which it is at most stimulus frequencies). A linear increase in the phase lag with increasing frequency suggests a fixed time delay between the stimulus and the response. The phase lag increases because the same fixed time delay represents a greater proportion of the shorter periods corresponding to the higher frequencies. The delay can be estimated from the regression slope of the phase response. Figure 3.6 shows that the phase roll-off varies with stimulus amplitude and rotation axis. The roll-off is significantly shallower for stimulus amplitudes of  $10^\circ$  than it is for amplitudes of  $2.5^\circ$  and  $5^\circ$  and this holds for the phase responses to roll ( $F_{2,198}=24.23$ ,  $p<0.001$ ), pitch ( $F_{2,182}=28.54$ ,  $p<0.001$ ) and yaw ( $F_{2,339}=28.39$ ,  $p<0.001$ ) stimuli. For the on-axis response to roll (figure 3.6, B), the estimated time delay is

$34 \pm 3$  ms (mean  $\pm$  95% confidence interval), and is not statistically distinguishable for the responses to stimuli of  $2.5^\circ$  and  $5^\circ$  amplitude ( $F_{1,158}=0.199$ ,  $p=0.656$ ). For a  $10^\circ$  amplitude, the time delay is  $21 \pm 9$  ms. For the on-axis phase response to pitch (figure 3.6, D), the estimated time delay is  $36 \pm 3$  ms for a  $2.5^\circ$  and  $5^\circ$  stimulus amplitude (with the same trend:  $F_{1,145}=2.473$ ,  $p=0.118$ ), and is  $19 \pm 9$  ms for a  $10^\circ$  stimulus amplitude. The slope of the on- and off-axis phase response to yaw stimuli (figures 3.6, F and H) is not statistically different ( $F_{1,339}=3.23$ ,  $p=0.073$ ). For the  $2.5^\circ$  and  $5^\circ$  amplitudes, the time delay for the on- and off-axis response is on average  $66 \pm 4$  ms, and for a  $10^\circ$  amplitude it is on average  $45 \pm 19$  ms. This shows that in response to yaw stimuli the time delay is roughly twice as long as for responses to roll and pitch stimuli, where the time delay is less than the wingbeat period of  $42 \pm 0.5$  ms.

The origin of the time delay includes the time required for biophysical processes, and also effects of internal damping which are caused by gating mechanisms, gaze stabilisation, thresholding effects, etc. The finding that the slope varies for different axes of rotation and for different stimulus amplitudes suggests that different motion vision processing pathways are used for different stimuli. Possible explanations could be the existence of parallel processing pathways with different control parameters (e.g. some pathways may be more affected by internal damping than others), or alternatively, an adaptive signal processing pathway (i.e. the control parameters vary as a function of the rotation axis and stimulus amplitude). These possibilities are not mutually exclusive. As mentioned in section 2.5, this analysis is performed under the assumption that the force transducer does not introduce any additional time lags (phase shifts).

### **3.7 Discussion**

The aim of this chapter was to assess the linearity of the optomotor system in response to roll, pitch and yaw stimuli. I found strong behavioural responses to double- and single-sine waveforms, comprising oscillation amplitudes of  $2.5^\circ$ ,  $5^\circ$  and  $10^\circ$ , and frequencies of 1 Hz to 12 Hz, 1+3 Hz, 3+4 Hz and characterised the optomotor system under the approximation of a quasi-linear system. I derive three main conclusions. First, the non-linear effect of stimulus amplitude is significant for apparent self-motion about all three cardinal axes and is faithfully reproduced in the describing functions presented in this chapter. Second, the response to yaw stimuli is strikingly different because i) it reveals a coupled moment response about the dorso-ventral axis; ii) its moment responses collapse onto one line when plotted against angular velocity; iii) it demonstrates a smaller useful working range; and iv), it has a significantly larger time delay. Third, the different time delays suggest that the system employs different control strategies, depending on the apparent body rotation axis.

Before I move on to the main discussion, I discuss the three potential caveats in the experimental design. First, the behaviour is measured from tethered moths. Tethered experiments disentangle the active and passive flight control by eliminating the aerodynamic effect of body and wing interaction with the surrounding air and are therefore key for the identification of the flight controller. It has been reported that the wingbeat frequency may be lower than in free flight and that the responses may be attenuated up to 65% [57] [58]. Hence, I might expect lower magnitude responses when compared to free flight, but I assume that the moth does not vary the physiological properties of the active controller in consequence of it being tethered. Second, I did not fix the head and therefore, the moths are able to perform gaze stabilisation. Hence, they can rotate their

head relative to the body and thereby reduce the angular velocity of retinal slip, i.e. they experience a smaller dynamic range than was projected onto the sphere. If I had fixed the head, the moths would have perceived a larger dynamic range and I would therefore expect the responses to have dropped sooner. The last caveat is that I used abstract stimuli with one fixed spatial frequency, rather than a large array of spatial frequencies that is apparent in natural scenes. In a natural scenery, the moth experiences a large range of contrast frequencies and the velocity tuning of the EMDs is less sensitive to textural pattern properties [54] [20]. Hence, the non-linear effect of amplitude may not be as pronounced in response to a natural scenery. Nonetheless, the aim of analysing linearity required the spatial frequency to be fixed and the contrast frequency to be constant across the entire visual field in order to expose the moth to a clearly defined and uniform motion pattern. In the remainder of this discussion I will focus on the components of the motion vision system that first, could cause the non-linear effect of stimulus amplitude which is independent of rotation axis; and second, that could cause the responses to yaw stimuli to differ so strongly from the responses to roll and pitch stimuli.

The consistent non-linear effect of stimulus amplitude is demonstrated by the fact that for stimulus frequencies greater than 4 Hz, larger stimulus amplitudes typically lead to smaller magnitude responses and to a shallower roll-off in the phase response. There are two reasons to assume why this effect is not caused by a limitation in the flight motor. First, if the stimuli would drive the motor to its limit, I would expect the system to maintain its maximum moment response. But no such saturation is observed in the moment responses in figure 3.8. Second, the maximum pitch and yaw rates of free flying *M. sexta* lie at  $1500^\circ/\text{s}$  [42] and  $1000^\circ/\text{s}$  [59] and therefore, the angular velocities of the stimuli lie within a range they are exposed to in free flight. Hence, I look for an explanation in the visual system. Because the non-linear behaviour is independent of rotation axis,

I suggest that the mechanism causing this response behaviour is at the level of local motion detection. Both a spatial and temporal anisotropy of the EMDs could lead to this amplitude-dependent non-linearity. A spatial anisotropy of EMDs suggests that the spatiotemporal comparison of brightness levels is not only performed across neighbouring ommatidia, but also with ommatidia that are located further away. Hence, smaller and larger stimulus amplitudes would activate different sets of EMDs. Such spatial anisotropy has already been found in flies [60]. A temporal anisotropy of EMDs suggests that the spatiotemporal comparison of brightness levels is performed by EMDs with different time constants, i.e. EMDs with different velocity optima. Hence, slower and faster stimuli can activate different sets of EMDs and hereby enhance the system's ability to respond to a larger range of velocities [61] [10]. Such temporal anisotropy has already been observed in crabs [15]. One main mechanism that could explain the distinct difference in the moment responses to roll, pitch and yaw stimuli is gaze stabilisation. Gaze stabilisation reduces the angular velocity of retinal slip and therefore allows the visual system to operate across a larger dynamic range of self-motion [20]. The responses in figure 3.8 may indicate that gaze stabilisation is performed well for roll and pitch stimuli, whereas gaze stabilisation is performed less well for yaw stimuli. Hence, the system responds to a larger range of stimulus parameters for roll and pitch motion, whereas the dynamic range of the yaw stimuli exceed the useful working range of the visual sensory system. An interesting point made by Ristroph et al. [62] is that yaw control may be designed to stabilise for the insect's state subsequent to passive stabilisation. The strong passive stabilisation of yaw motion that is addressed by Ristroph et al. could have various implementations in the design of the controller: Because of the high rate damping, the system may not need to generate a fast response to yaw stimuli and therefore the time delay of that particular controller is relatively large. Or, as will be discussed in next chapter, rate feedback is

taken care of by this aerodynamic damping.

### **3.8 Conclusion and outlook**

I conclude that the non-linear effect of stimulus amplitude which is consistent for roll, pitch and yaw stimuli could be caused by a spatial or temporal anisotropy of the EMDs. And, the different response behaviours and dynamic working ranges that we observe for roll, pitch and yaw stimuli could be explained by the limited ability to perform gaze stability in response to yaw motion.

The fact that the non-linear effect of the stimulus amplitude is manifested at the level of flight behaviour may indicate its importance to flight control and stabilisation. On the other hand, the non-linearities manifested in this partial open-loop setup may not be significant for the functioning of the closed loop system, i.e. for a free flying moth. This is because in a closed loop system with reasonable feedback, a local equilibrium is reached. Hence, the feedback keeps the system near to equilibrium where it can operate within a linear framework.

In the next chapter I will focus on the effect of changing the rotation axis of the stimulus on the behavioural responses. Hence, I will explore how the flight control mechanism changes for different spatial composition of optic flow.

## Chapter 4

# Testing spatial superposition of the optomotor responses with linear control models

The previous chapter concludes that there is a non-linear effect of stimulus amplitude on the optomotor responses, especially for the response to yaw stimuli. This could be due to either a pure effect of amplitude (e.g. spatial anisotropy of EMDs, or limited ability of gaze stabilisation), or, due to the sensitivity of the system to angular rates (e.g. temporal anisotropy of EMDs). In either case, finding the cause for this non-linear effect of amplitude would require a more detailed understanding of the gaze stabilisation and the arrangement of EMDs. The measurements discussed in previous chapter also showed that the optomotor responses vary as a function of the rotation axis of the stimulus. This is the aspect I will focus on in this chapter. Hence, I fix the stimulus amplitude to  $5^\circ$  and study the effect of rotation axis on the optomotor responses in more detail.

In their natural setting, moths experience a variety of aerial disturbances and therefore

their motion vision system needs to cope with complex patterns of rotational optic flow. This chapter addresses spatial superposition which is a potential mechanism that enables the visual system to deal with this variety in optic flow patterns. As mentioned in the introduction of this thesis, wide-field motion-sensitive and direction-selective interneurons (LPTCs) have been found in flies. Each LPTC encodes optic flow from a subarea of the visual field, suggesting that wide-field optic flow is broken down into subcomponents and that each subcomponent yields an individual response. These individual responses from these individual LPTCs are then integrated to generate the vision-based command to the flight motor. Spatial superposition means that the sum of the responses to separate flow fields should correspond to the response to the sum of the flow fields. Hence, the basic idea is that a complex pattern of optic flow is divided into subunits. And the response to the complex pattern is equal to the sum of the responses generated for these individual subunits. Previous studies explored the superposition of looming, translational and rotational flow fields. For instance, Duistermars et al. [3] studied the superposition of expanding and rotating flow fields and concluded that although optic flow is perceived by the same EMDs the responses are likely to be mediated by two separate pre-motor circuits. Theobald et al. [6] suggest that the optomotor responses to translational and rotational flow fields are mediated by two parallel pathways, and that linear superposition explained a large portion of the responses. If spatial superposition is performed in *M. sexta*, I should be able to predict the responses to rotational stimuli about an arbitrary axis by superposing the responses to rotational stimuli about other axes. In order to address this question, I expand the dataset from the previous chapter and use the same tethered setup to measure the optomotor responses to single-sine oscillations of  $5^\circ$  amplitude and frequencies of 1, 2, 3, 4, 6, 8 and 12 Hz about three new stimulus axes  $x'$ ,  $z'$ , and  $x''$ . As shown in figure 2.3, the  $x'$ - and  $z'$ -axes coincide approximately with the principal

axes of the body within the moth's plane of symmetry. The  $x''$ -axis lies at an angle of  $45^\circ$ , intermediate to the  $x$ - and the negative  $y$ -axis. Note how stimuli about the  $x''$ -axis combine longitudinal and lateral motion.

This chapter is structured as follows: In section 4.1, I present all frequency responses discussed in this chapter, i.e. the responses to 42 single-sine stimuli with a  $5^\circ$  stimulus amplitude. There is a significant difference in how I represent the response behaviour compared to the previous chapter. From here on and for the rest of this thesis, I treat the visual input to the system as the angular rate rather than angular position. As we have seen in the previous chapter, treating the angular position as input helps clarifying particular questions such as the effect of stimulus amplitude on the responses. Treating the angular rate as input on the other hand is closer to the physiological behaviour (e.g. EMDs are sensitive to the velocity of the optic flow). Both approaches are found in literature and the two treatments are equivalent. Hence, the visual stimuli for the six different rotation axes are from now on referred to as changes in angular rates  $p$  for oscillations about the  $x$ -axis,  $q$  for oscillations about the  $y$ -axis,  $r$  for oscillations about the  $z$ -axis,  $p'$  for oscillations about the  $x'$ -axis,  $r'$  for oscillations about the  $z'$ -axis, and  $p''$  for oscillations about the  $x''$ -axis (figure 2.3). In section 4.2, I introduce the theory of linear control models. In section 4.3, I fit a family of linear control models to the optomotor responses. These vision-based flight control models contain the gains on the visual feedback parameters (i.e. the stimulus rate and its integral and derivative components) and the time delay of the optomotor system. I then test spatial superposition in two ways. First, in section 4.4, I linearly superpose the control models for the lateral roll motion  $p$  and the longitudinal pitch motion  $q$  in order to predict the optomotor responses to  $p''$ . Second, from section 4.5 onward, I test spatial superposition by lumping all the optomotor responses for all lateral stimuli ( $p$ ,  $r$ ,  $p'$  and  $r'$ ). I herewith analyse to what extent a generalised control model is

capable of explaining the variation in responses caused by the changes in stimulus axis. Hence, I explore to what extent the control law for lateral stimuli can be generalised. As we will see, there is no general control law that can explain the responses to an arbitrary lateral stimulus. Therefore, the motion vision pathway does not operate according to spatial superposition for lateral motion.

## 4.1 Frequency responses with the stimulus velocity as input signal

The moths generated high response power with a coherence  $\geq 0.6$  at the fundamental temporal frequency of the 21 new stimuli (figures C.1, C.2 and C.3). Some response power was generated at the harmonic frequencies of 4 Hz and 6 Hz for stimuli  $r'$  and  $p''$ . In order to test whether this harmonic response power was related to the stimulus, I calculated the coherence at those harmonic frequencies by generating an artificial stimulus that contained power at those frequencies with an amplitude proportional to the stimulus at the fundamental frequency. The coherence values of the harmonic response power at 8 Hz and 12 Hz was below 0.6 and therefore not attributable to the stimulus. Hence, just like in the previous chapter, I will characterise the system based on the assumption of quasi-linearity.

Figures 4.1, 4.2 and 4.3 show the frequency responses for all 42 single-sine stimuli (table 4.1) from which I will later on derive the vision-based flight control models.

In each of these figures, the top graph shows the total mean coherence of the roll, pitch and yaw response moments and the total number of trials for each stimulus. Each response moment with a total mean coherence  $\geq 0.6$  is then characterised in terms of the mean magnitude response in the middle graph, and in terms of the mean phase response

**Table 4.1:** A total of 42 stimuli are used to analyse the spatial superposition of the optomotor responses. The single-sine stimuli have a fixed stimulus amplitude of  $5^\circ$  and their frequency varies from 1 Hz to 12 Hz. The spatial composition of the optic flow varies as a function of the rotations axis.

| Rotation axis        | Amplitude (max, $^\circ$ ) | Frequency (Hz)       |
|----------------------|----------------------------|----------------------|
| x, y, z, x', z', x'' | 5                          | 1, 2, 3, 4, 6, 8, 12 |

in the bottom graph. The magnitude is normalised with the moth's mass. Each individual trial that contributes to the mean magnitude and phase values has a coherence  $\geq 0.6$ . For longitudinal stimuli  $q$ , the pitch moment dominates the response. For the four lateral stimuli  $p$ ,  $r$ ,  $p'$  and  $r'$ , the moths always generate a coupled response consisting of a roll and yaw moment. Note that the magnitude responses for stimuli  $r$  and  $p'$  are smaller than the magnitude responses for  $p$  and  $r'$ . The 1 Hz oscillation about the x'-axis (stimulus  $p'$ , 1 Hz) was erroneous as one out of 144 frames was missing. Nonetheless, the coherence of the yaw moment response is  $\geq 0.6$  and I assume that this error of 0.0069 s did not significantly affect the moth's response behaviour. In response to  $p''$ , i.e. stimuli that combine longitudinal and lateral motion, the roll and the pitch moments dominate the responses. There is also a yaw response moment with a total mean coherence  $\geq 0.6$  for three out of seven frequencies. This is not surprising considering the coupled responses that are generated in response to lateral stimuli.

As already done in the previous chapter, I plot the normalised mean moment responses as a function of the mean angular velocity of the stimulus. Figure 4.4 shows the normalised mean moment responses for all 42 stimuli.

Note that all trials that contribute to the mean moment responses have a coherence  $\geq 0.6$ . The moment responses illustrated in figure 4.4 are indicative of how sensitive the system is to the angular rate of the stimulus. The increase of the yaw moment response  $N$  with angular velocity (e.g. in figure 4.4, C and D) suggests that the moth is relying

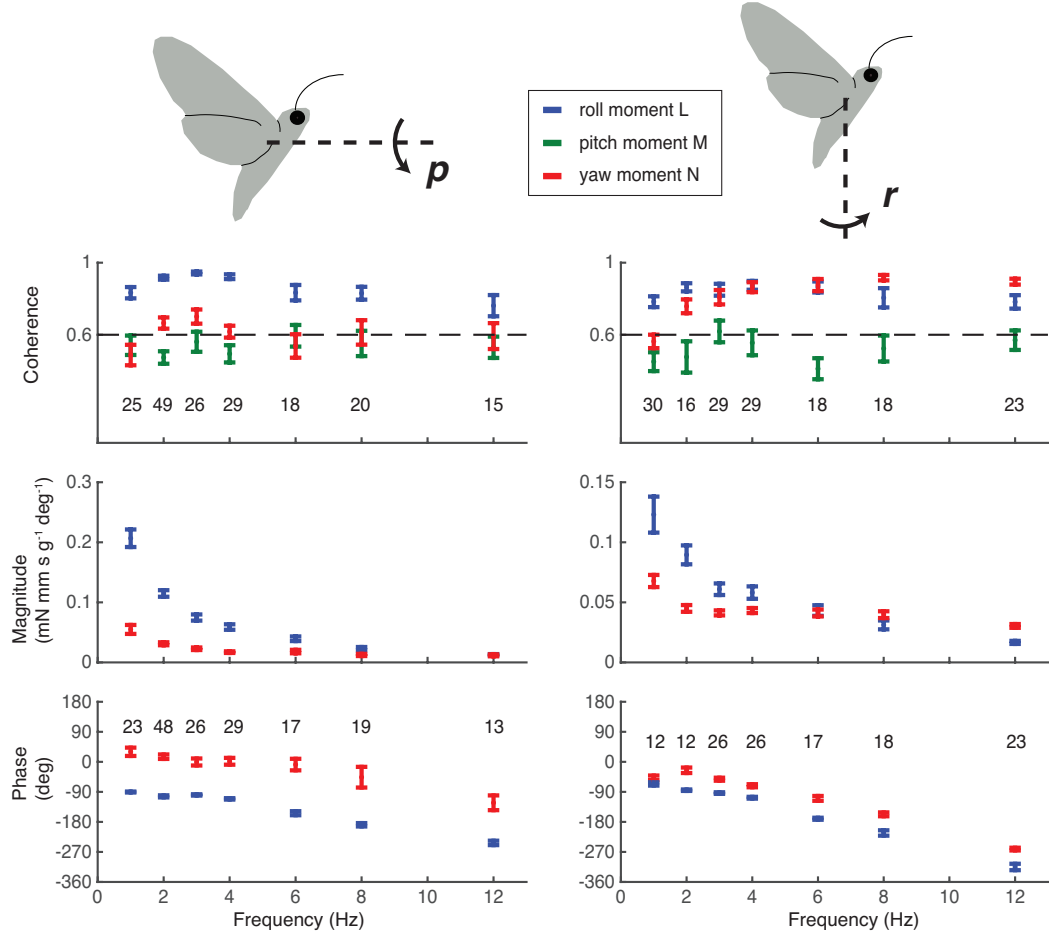


**Figure 4.1:** Measured frequency responses for the lateral stimuli  $p$  (left column) and  $r$  (right column). All stimuli are single-sine oscillations with a  $5^\circ$  stimulus amplitude and frequencies between 1 and 12 Hz. Data points show means of the individual means  $\pm$ SEM. The top graph shows the total mean coherence for the roll (blue), pitch (green) and yaw (red) response moments. The numbers in the top graph indicate the total number of trials per stimulus. The middle graph shows the mean magnitude responses. The bottom graph shows the mean phase responses. The magnitude and the phase are defined relative to the mean angular rate of the stimulus. The numbers in the bottom graph indicate the number of trials with a coherence  $\geq 0.6$  along the stimulus axis  $x$  or  $z$ , respectively.

on the feedback of rate information to generate its moment response. In the next section I will refer to this as a proportional feedback, or a proportional controller, because the

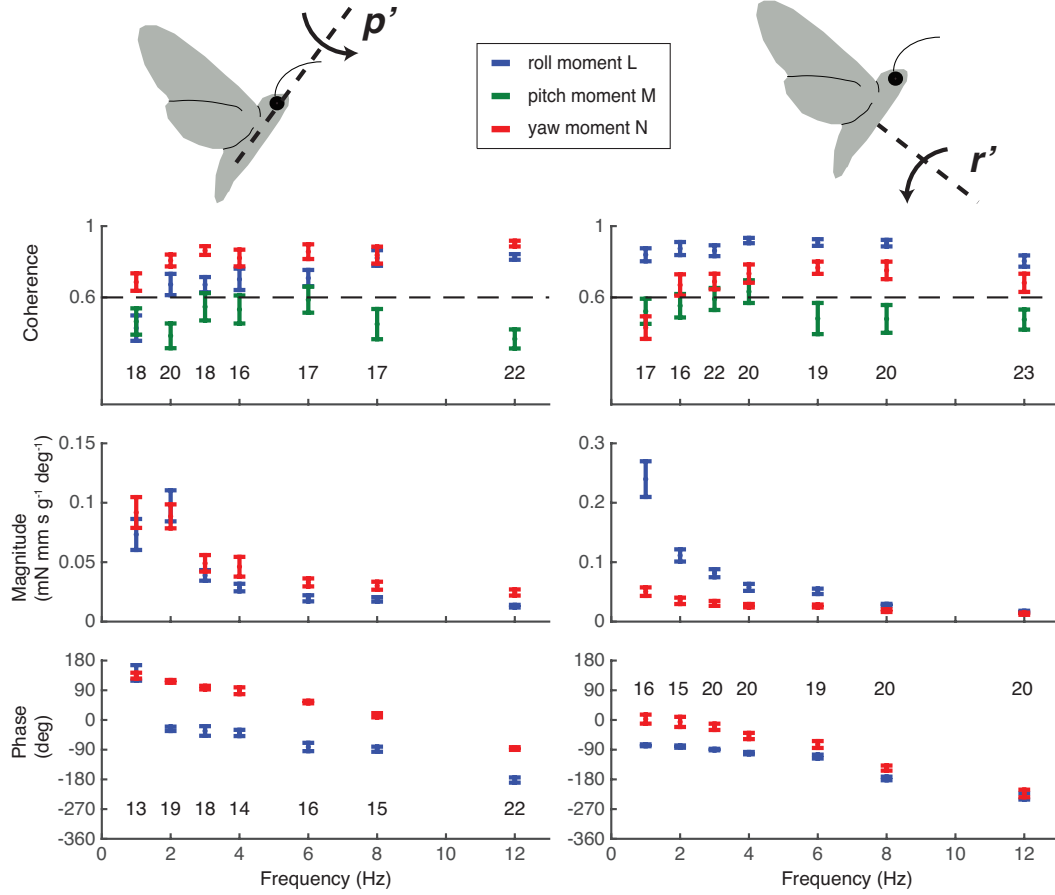


**Figure 4.2:** Measured frequency responses for the lateral stimuli  $p'$  (left column) and  $r'$  (right column). All stimuli are single-sine oscillations with a  $5^\circ$  stimulus amplitude and frequencies between 1 and 12 Hz. Data points show means of the individual means  $\pm$ SEM. The top graph shows the total mean coherence for the roll (blue), pitch (green) and yaw (red) response moments. The numbers in the top graph indicate the total number of trials per stimulus. The middle graph shows the mean magnitude responses. The bottom graph shows the mean phase responses. The magnitude and the phase are defined relative to the mean angular rate of the stimulus. The numbers in the bottom graph indicate the number of trials with a coherence  $\geq 0.6$  along the z- and x-axis, respectively.

response is proportional to the angular velocity. On the other hand, the relatively flat curve of the roll moment responses  $L$  (e.g. in figure 4.4, A and E) suggests that the moth is using feedback of angular position rather than angular rate in order to generate the

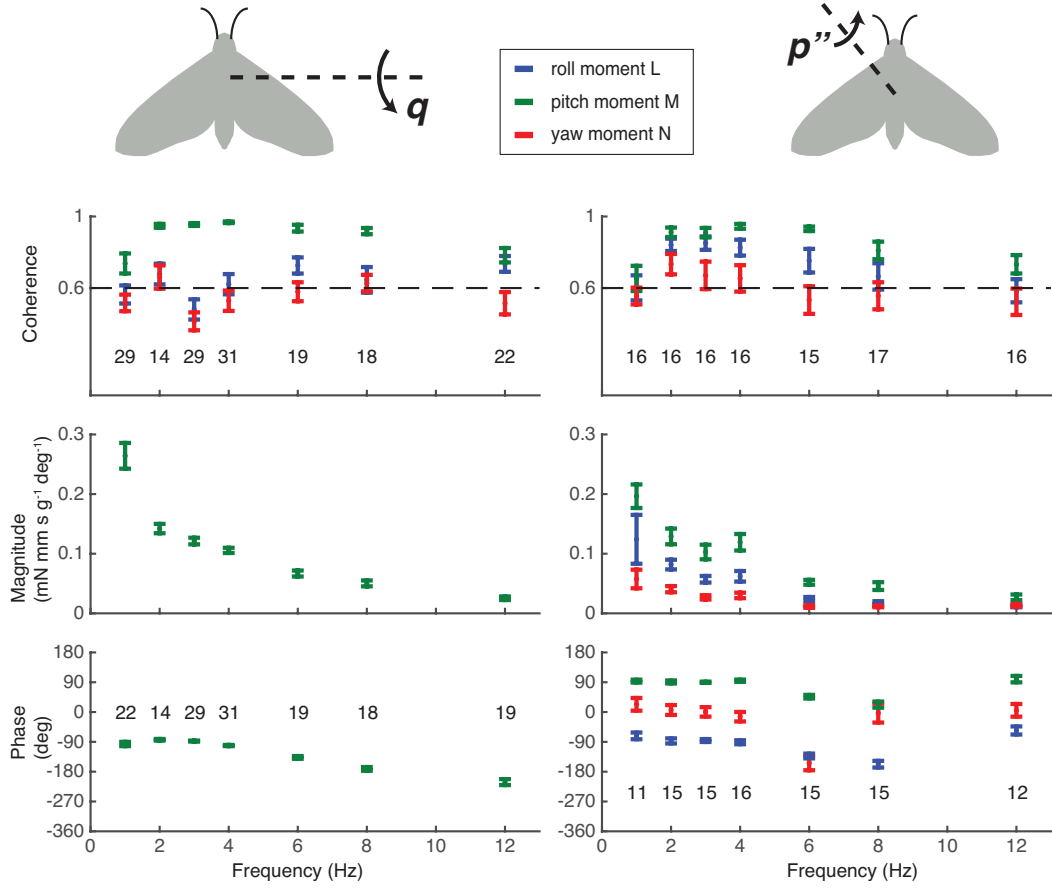


**Figure 4.3:** Measured frequency responses for the stimuli  $q$  (left column) and  $p''$  (right column).  $q$  simulates a pure longitudinal pitch rotation, whereas  $p''$  simulates a combined longitudinal and lateral motion. All stimuli are single-sine oscillations with a  $5^\circ$  stimulus amplitude and frequencies between 1 and 12 Hz. Data points show means of the individual means  $\pm$ SEM. The top graph shows the total mean coherence for the roll (blue), pitch (green) and yaw (red) response moments. The numbers in the top graph indicate the total number of trials per stimulus. The middle graph shows the mean magnitude responses. The bottom graph shows the mean phase responses. The magnitude and the phase are defined relative to the mean angular rate of the stimulus. The numbers in the bottom graph indicate the number of trials with a coherence  $\geq 0.6$  along the y-axis.

moment response. In the next section I will refer to this as an integral feedback, or an integral controller, because the response is proportional to the integral of angular velocity.

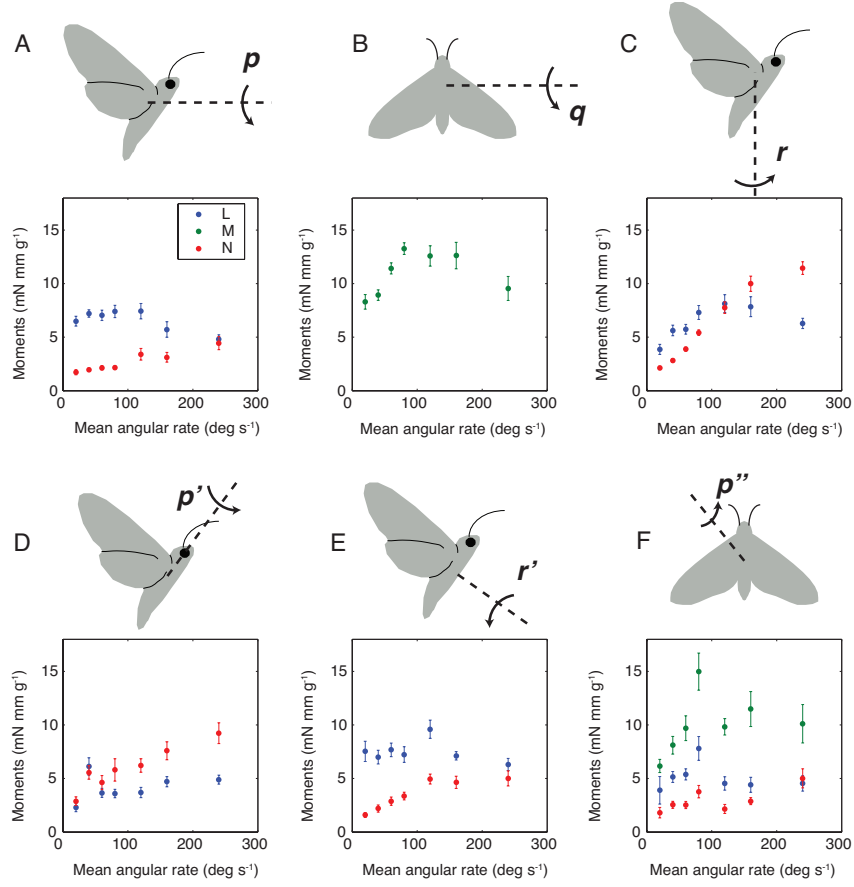


**Figure 4.4:** Normalised moment responses to stimuli  $p$  (A),  $q$  (B),  $r$  (C),  $p'$  (D),  $r'$  (E), and  $p''$  (F), plotted as a function of the mean angular rate of the stimulus. All stimuli are single-sine oscillations with a  $5^\circ$  stimulus amplitude and frequencies between 1 and 12 Hz. The colours indicate the roll (blue), pitch (green) and yaw (red) moment responses. Data points show means of the individual means  $\pm$ SEM.

Now that I am confident that a quasi-linear approach is valid and that all responses for these 42 stimuli are strongly related to the stimulus, I fit control models to these frequency responses. This model identification will show what visual parameters and time delays are being used in order to visually control different classes of apparent body rotations. Subsequently, these control models will allow me to explore the mechanisms of spatial superposition. But first, I explain the theory of linear control models and the model

fitting process in the following section.

## 4.2 Linear control theory

The optomotor response is the dynamic relationship between the response moments and the visual stimulus. Because of the tethered setup, the response moments correspond to the controller's output  $u(t)$  in figure 4.5. The visual stimulus indicates the offset from an equilibrium where all rotational motion is zero and therefore indicates the measured error  $\epsilon(t)$  in figure 4.5. The role of the controller is to modify the control signal  $u(t)$  to counteract the error signal  $\epsilon(t)$  and to bring the system back to rotational equilibrium ( $p = q = r = p' = r' = p'' = 0$ ). Hence, the control signal  $u(t)$  that is passed on to the physical system (the flying moth) strongly depends on the properties of  $\epsilon(t)$ . The controller essentially corresponds to the central nervous system which selects the control-relevant parameters from the visual scenery and combines it with sensory feedback from other modalities in order to then generate the control signal  $u(t)$ . Equation 4.1 shows the most common controller used in linear control theory (LCT):

$$u(t) = K_P \cdot \epsilon(t - \tau) + K_I \cdot \int_0^t \epsilon(t' - \tau) dt' + K_D \cdot \frac{d\epsilon(t - \tau)}{dt} \quad (4.1)$$

It computes  $u(t)$  as the sum of the proportional (P), integral (I) and derivative (D) components of  $\epsilon(t)$  [63].  $\tau$  corresponds to the time delay between the stimulus  $\epsilon(t)$  and the response  $u(t)$ . The first term of equation 4.1 contains  $K_P$ , which is a gain proportional to  $\epsilon(t)$  and therefore quantifies feedback of angular rate. The two other gains  $K_I$  and  $K_D$  depend on the dynamic properties of  $\epsilon(t)$ .  $K_I$  is a gain which is proportional to the time integral of  $\epsilon(t)$  and therefore quantifies the feedback of angular position.  $K_D$  is a gain which is proportional to the temporal derivative of  $\epsilon(t)$  and therefore quantifies the

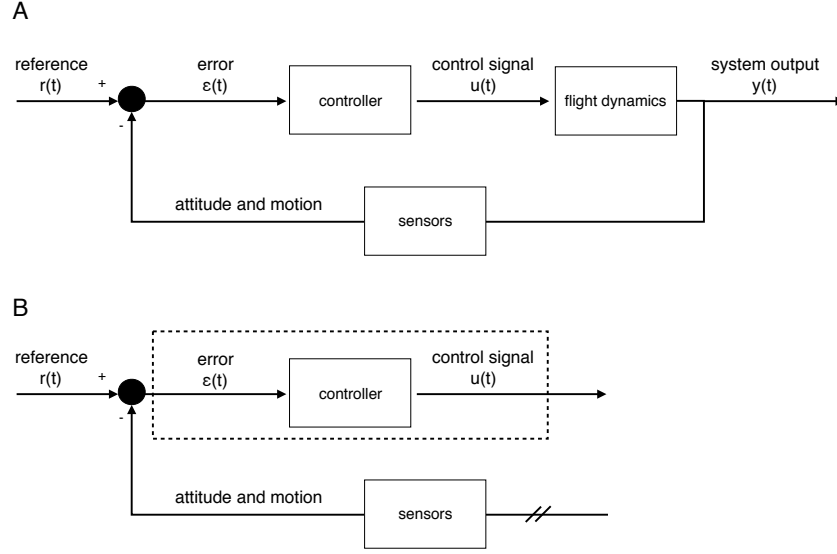


**Figure 4.5:** Schematic of the flight control system. (A) The top graph illustrates the closed-loop system where sensory feedback provides a description of the moth's state (i.e. attitude and motion) in space. This state is then compared to the reference state  $r(t)$ . Any involuntary offset leads to an error  $\epsilon(t)$ . The properties of this error signal drive the control signal  $u(t)$ . The controller sends the signal  $u(t)$  to the physical body, where the flight dynamics are modulated in order to minimise the error  $\epsilon(t)$  and converge to the reference point  $r(t)$ . Hence, the role of the flight controller is to modulate the control signal  $u(t)$  so as to drive the error  $\epsilon(t)$  to zero. (B) The bottom graph illustrates the tethered setup where sensory feedback corresponds to the state simulated by the visual stimuli. I assume that proprioceptive feedback is non-existent or consistently erroneous, and except for gaze stabilisation, the moths have no control over the visual stimulus. The apparent motion is the error  $\epsilon(t)$  from a rotational equilibrium  $r(t)$ . This error initiates a control signal  $u(t)$  which in turn modifies the aerodynamic moment responses of the moth. Hence, I measure the control signal that the moths generate in response to an apparent body rotation. The tethering prevents the control signal  $u(t)$  from interfering with the flight dynamics and therefore does not change the moth's state. The dashed line outlines the part of the system I am interested in identifying in this chapter. The optomotor response is the dynamic relationship of the measured control signal  $u(t)$  and the error, i.e. the controlled visual stimulus  $\epsilon(t)$ . The fitted linear control model describes this relationship in a mathematical form and gives an approximation of the vision-based flight stabilisation and control in *M. sexta*.

feedback of angular acceleration. Lets take equation 4.2 as an example.

$$M(t) = K_P \cdot q(t - \tau) + K_I \cdot \theta(t - \tau) + K_D \cdot \dot{q}(t - \tau) \quad (4.2)$$

$u(t)$  is the pitch moment response  $M(t)$  and it is a function of the pitch rate  $q(t)$  of the stimulus (i.e. proportional to the error signal  $q(t)$ ), the pitch angle  $\theta(t)$  (i.e. proportional to the accumulated error which is the time integral of  $q(t)$ ), and the angular acceleration  $\dot{q}(t)$  (i.e. proportional to the rate of change of the error which is the time derivative of  $q(t)$ ). I set  $u(t) = M(t)$  under the assumption that the dynamic properties of the force transducer are not relevant and that therefore the moment measured in the tethered preparation fully and solely corresponds to the control moment.

In general, the control parameters  $K_P$ ,  $K_I$ ,  $K_D$  are tuned for a particular range of input  $\epsilon(t)$ . If the controller receives an input which lies outside of its functional range, i.e. if the time delay or the gains of the controller are not designed for a large enough range of  $\epsilon(t)$ , the PID elements can introduce non-linearities such as saturation, rectification, etc. The frequency domain representation is more compact than plotting up all of the input-output pairs in the time domain. I therefore transform each term of equation 4.1 into the frequency domain by applying the Laplace transform  $\mathcal{L}$  with the complex frequency  $s = j2\pi f$  (rad s<sup>-1</sup>) and  $j = \sqrt{-1}$  [53]. Equation 4.3 shows the Laplace transform of the time delayed input:

$$\mathcal{L} [\epsilon(t - \tau)] = E(s)e^{-s\tau} \quad (4.3)$$

Hence, in the frequency domain, the time delay is now represented by an exponential function of the complex frequency  $s$  and the delay  $\tau$ . Equation 4.4 shows the Laplace transform of the integral function:

$$\mathcal{L} \left[ \int_0^t \epsilon(t' - \tau) dt' \right] = \frac{1}{s} E(s) e^{-s\tau} \quad (4.4)$$

And equation 4.5 shows the Laplace transform of the derivative function:

$$\mathcal{L} \left[ \frac{d\epsilon(t - \tau)}{dt} \right] = s E(s) e^{-s\tau} \quad (4.5)$$

These three terms are then recombined to form the general function of a PID-controller in equation 4.6 which is much easier to manipulate and to solve. Equation 4.6 is a key equation in this thesis as it shows the structure of the flight control models I am about to fit to the optomotor responses.

$$U(s) = \left( K_P + K_I \cdot \frac{1}{s} + K_D \cdot s \right) E(s) e^{-s\tau} \quad (4.6)$$

The schematic of the PID-controller is shown in figure 4.6.

Each of the three control terms has a benefit and a potential cost to the system that is being controlled. And, each of the three control terms has a different effect on the magnitude and phase as illustrated in figure 4.7.

An increase in  $K_P$  increases the speed of control. But if  $K_P$  is too large, the system can begin to oscillate and become unstable. As explained in the previous section, the presence of a proportional controller is indicated by a constant magnitude (figure 4.7, A), because if the moment response relies on proportional feedback of angular rate, then the moment response will increase proportionally with the stimulus frequency. If  $K_I$  is chosen too small, the controller can cause overshoot or oscillations. The integral accumulates the error and therefore grows over time unless  $\epsilon(t)$  is zero. This potentially leads to non-linear effects such as integrator saturation. An integral feedback is represented by a decaying magnitude (figure 4.7, C) because the moment response will remain constant as

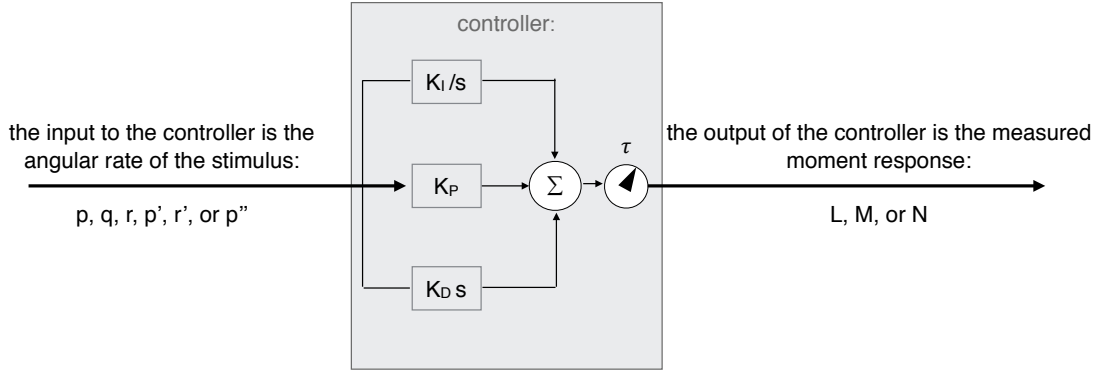


**Figure 4.6:** Schematic of the PID-controller with an input  $E(s) = p, q, r, p', r'$  or  $p''$  and an output  $U(s) = L, M$  or  $N$ . The input to the controller is the angular rate of the stimulus. The output of the controller is the response moment measured by the force balance. The PID-controller has three parallel pathways: one that controls the feedback of angular rate ( $K_P$ ), one that controls the feedback of angular position ( $K_I/s$ ), and one that controls the feedback of angular acceleration ( $K_D s$ ). The time delay  $\tau$  is the delay of the optomotor response. In free flight, the control output  $u(t)$  would be fed to the physical system to modify the moth's flight dynamics such as to counterbalance the apparent motion  $E(s)$ .

the frequency of the stimulus increases. The integral feedback introduces a phase lag of  $-90^\circ$  and has a low-pass filtering effect (figure 4.7, D), meaning that it will pass on slow changes and smoothen a longterm trend in the signal. The derivative feedback has a high-pass filtering effect and therefore eliminates DC components and passes on fast changing, high frequency components of  $\epsilon(t)$  (figure 4.7, E). The derivative feedback advances the phase by  $+90^\circ$  (figure 4.7, F) and anticipates the future behaviour of  $\epsilon(t)$ . But the derivative feedback is highly sensitive to noise. For instance, if the rate of change of  $\epsilon(t)$  is very high due to random fluctuations,  $K_D$  will strongly amplify noise and potentially lead to inappropriate control responses. Hence,  $K_D$  is usually kept small to prevent the system from getting unstable.

In the next step I want to find the feedback gains  $\mathbf{K} = [K_P, K_I, K_D]^T$  and the time delay  $\tau$  that best explain the dynamic relationship between the output  $U(s)$  and the input

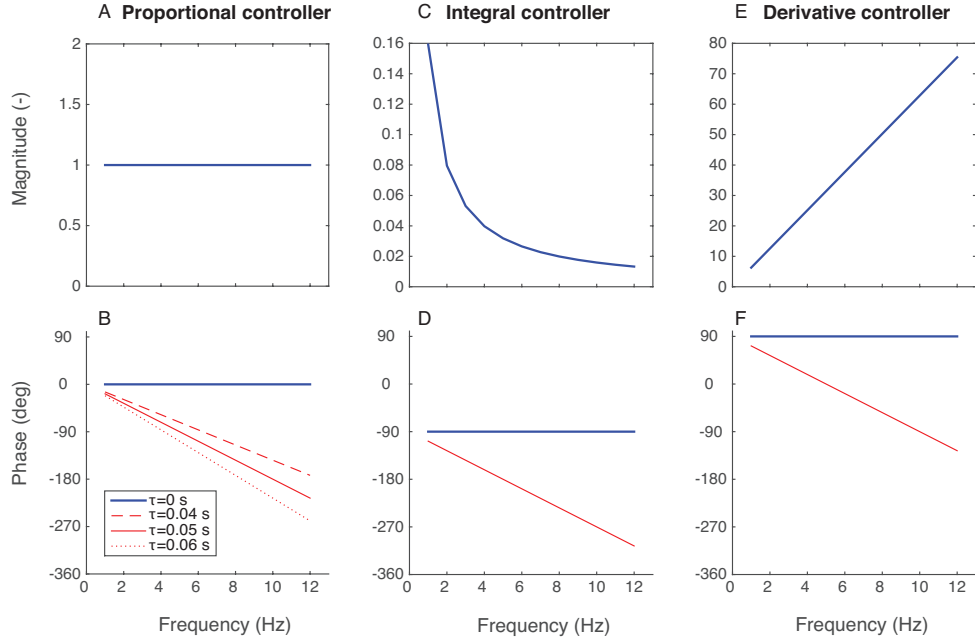


**Figure 4.7:** Frequency response plots of the proportional feedback  $K_P = 1$  (A-B); of the integral feedback  $K_I = \frac{1}{s}$  (C-D); and of the derivative feedback  $K_D = s$  (E-F). The effect of adding a time delay term  $e^{-s\tau}$  is limited to the phase only and elicits a linear increase in the phase lag with increasing frequency (B). A larger time delay leads to a steeper phase roll-off.

$E(s)$  that is shown in equation 4.6. This dynamic relationship can also be represented by the transfer function  $H(s)$  in equation 4.7:

$$H(s) = \frac{U(s)}{E(s)} \quad (4.7)$$

A transfer function is a complex function and always only represents the dynamic relationship of one input to one output. Therefore, given an input  $E = p, q, r, p', r'$  or  $p''$  with a complex frequency  $s = j2\pi f$ , then  $H(s)$  is defined for each individual moment response  $U = L, M$  or  $N$ . I define the model transfer function  $H(s)$  in equation 4.8:

$$H(s) = \left( K_P + K_I \cdot \frac{1}{s} + K_D \cdot s \right) e^{-s\tau} \quad (4.8)$$

This PID-model, or controller, describes the optomotor response as a function of the visual parameters (angular rate, angular position, angular acceleration) and the time delay  $\tau$ . The measured transfer function  $H(f)$  in equation 4.9 is generated by recombining the mean magnitude and phase values at a particular frequency  $f$ .

$$H(f) = \text{mag}(f) \cdot e^{j \cdot \text{phase}(f)} \quad (4.9)$$

In the next step, I fit the model transfer function  $H(s) = \mathbf{xK}$  to the measured transfer functions  $H(f) = \mathbf{Y}$  and resolve for the gains in vector  $\mathbf{K}$  and the time delay  $\tau$ :

$$\mathbf{Y} = \mathbf{xK} = \begin{bmatrix} e^{-s_1\tau} & \frac{1}{s_1}e^{-s_1\tau} & s_1e^{-s_1\tau} \\ \vdots & \vdots & \vdots \\ e^{-s_7\tau} & \frac{1}{s_7}e^{-s_7\tau} & s_7e^{-s_7\tau} \end{bmatrix} \begin{bmatrix} K_P \\ K_I \\ K_D \end{bmatrix} \quad (4.10)$$

The predictor matrix  $\mathbf{x}$  in equation 4.10 contains three columns, representing the proportional, integral and derivative components of the visual input  $E_{in}(s)$  for the seven complex frequencies  $s_i = j2\pi f_i$ , where the subscript  $i$  indicates the seven frequencies  $f_i = 1, 2, 3, 4, 6, 8$  or 12 Hz. Each column in  $\mathbf{x}$  represents a parameter of the visual stimulus that the controller may use to stabilise the system. For instance, if the input to the system is a roll rate  $p$ , then the controller may use a combination of  $p$ , its integral  $\phi$ , and its derivative  $\dot{p}$  in order to generate the response moment and counterbalance the apparent error. In order to derive a family of potential controllers I alternately set the predictors for  $K_P$ ,  $K_I$  and  $K_D$  to zero and thereby define seven competing models: PID, PD, PI, ID, P, D, and I. Hence, I am fitting the optomotor responses with an array of models that contain the feedback of different visual parameters.

When I fit a model, I first iterate over the time delay from  $\tau=0$  s in steps of 0.002 s to  $\tau=0.2$  s. For each iteration,  $\tau$  is inserted into the predictor matrix  $\mathbf{x}$  and hereby

renders equation 4.10 which is nonlinear in  $\tau$  to one that is linear. I solve  $\mathbf{Y} = \mathbf{xK}$  with the linear least squares method and identify  $K_P$ ,  $K_I$ , and  $K_D$  for each iteration of  $\tau$ . The MATLAB function *lskov* solves the ordinary least squares problem  $\mathbf{Y} = \mathbf{xK}$  by weighting the residuals with the inverse of the sample variance  $\sigma^2$ . The sample variance is the covariance of all measured transfer functions  $H(f_i)$  for a particular stimulus  $E(s_i)$ , response moment  $U(s_i)$  and stimulus frequency  $f_i$ , divided by the sample size. Weighting the residuals with the inverse of the sample variance takes into account the variation in sample size. After having iterated over  $\tau$ , I select the time delay that minimises the mean squared error, i.e. the least square estimate of error variance. This delay is then set as an initial estimate  $\tau_0$  and is then further optimised with the MATLAB function *fmincon*. This nonlinear algorithm finds the time delay that minimises the mean squared error by starting at the initial estimate of  $\tau_0$  and by using a Hessian active-set algorithm to find a solution within the boundaries of  $\tau=0$  s and  $\tau = \tau_0+0.04$  s. *fmincon* delivers the optimised time delay, the gains and the mean squared error of the model (e.g. table 4.2).  $K_P$ ,  $K_I$  and  $K_D$  are the gains on the visual feedback parameters and have the units of mN mm s g<sup>-1</sup>deg<sup>-1</sup>, mN mm g<sup>-1</sup>deg<sup>-1</sup>, and mN mm s<sup>2</sup>g<sup>-1</sup>deg<sup>-1</sup>, respectively. The Small Sample Corrected Akaike Information Criterion (AICc, explained in section 2.6) rates the performance of the seven competing models (e.g. table 4.2) and indicates the best model with the smallest AICc.  $k$  is the total number of estimated model parameters which in this case comprises a term for the fitted time delay, a term to account for the error variance, and  $r$ , the number of parameters (gains) estimated in the linear regression. The error sum of squares SSE is calculated according to equation 4.11, whereby MSE is the mean squared error, and  $r$  is the number of estimated parameters in the linear regression.

$$\text{SSE} = \text{MSE} \cdot (n - r) \quad (4.11)$$

### 4.3 Fitting a linear control model to the individual response moments

First, I fit the family of seven competing models (PID, PD, PI, ID, P, D, and I) to the pitch response moment  $M$  generated in response to pitch stimuli  $q$ . The transfer function  $H_{M,q}(s)$  describes the dynamics of this single-input, single-output (SISO) system:

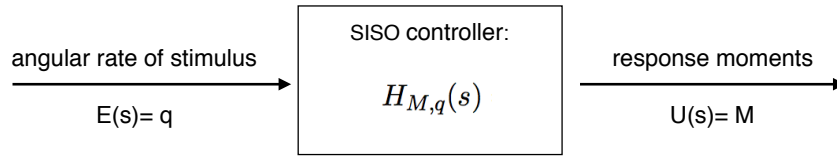


**Figure 4.8:** The controller  $H_{M,q}(s)$  describes the dynamic relationship of the pitch response moment  $M$  generated in response to pitch rate  $q$ .

In table 4.2, the performance of each model is represented by the AICc value. The model that best describes the pitch dynamics (i.e. the model with the lowest AICc) is a PI-controller with a time delay of 0.042 s.  $K_q$  is the gain on the pitch rate  $q$  of the stimulus,  $K_\theta$  is the gain on the pitch angle  $\theta$  of the stimulus, and  $K_{\dot{q}}$  is the gain on the pitch angular acceleration  $\dot{q}$  of the stimulus. The corresponding control algorithm is given in equation 4.12.

$$H_{M,q}(s) = \left( 0.053 + 1.472 \frac{1}{s} \right) e^{-s0.042} \quad (4.12)$$

I obtained the corresponding 95% confidence intervals for the control gains (table 4.3) by applying a basis transformation to the measured responses  $\mathbf{Y}$  and the predictor matrix  $\mathbf{x}$ . I applied this transformation so that they meet the assumptions of the general least squares in order to then apply a linear regression to obtain the confidence intervals (details are provided in section C.2).

**Table 4.2:** Results of the AICc analysis for the seven candidate models fitted to the optomotor responses to  $q$ . The 14 datapoints correspond to the seven mean magnitude and phase responses in the left graph of figure 4.3. The transfer function  $H_{M,q}(s)$  is best fitted by a PI-controller with a time delay of 0.042 s.

| controller    | PID       | PD        | PI       | ID       | P        | D        | I        |
|---------------|-----------|-----------|----------|----------|----------|----------|----------|
| k             | 5         | 4         | 4        | 4        | 3        | 3        | 3        |
| n             | 14        | 14        | 14       | 14       | 14       | 14       | 14       |
| AICc          | 59.01493  | 70.42168  | 53.95937 | 58.33897 | 66.37724 | 72.68845 | 54.4862  |
| Lh            | 0.079836  | 0.000266  | 1        | 0.111939 | 0.002011 | 8.57E-05 | 0.768422 |
| $\tau$        | 0.042     | 0.061     | 0.042    | 0.014    | 0.061    | 0.026    | 0.015    |
| $K_q$         | 0.052892  | 0.057091  | 0.052896 | 0        | 0.057091 | 0        | 0        |
| $K_\theta$    | 1.471984  | 0         | 1.471917 | 2.0974   | 0        | 0        | 1.989051 |
| $K_{\dot{q}}$ | -8.33E-08 | -7.44E-10 | 0        | 0.000126 | 0        | -0.00085 | 0        |

**Table 4.3:** The lower and upper boundary of the 95% confidence interval for the control gains of  $H_{M,q}(s)$ .  $K_q$  is the gain on the stimulus pitch rate  $q$ ,  $K_\theta$  is the gain on the pitch angle  $\theta$ , and  $K_{\dot{q}}$  is the gain on pitch angular acceleration  $\dot{q}$ .

|               |        |        |
|---------------|--------|--------|
| $K_q$         | 0.0341 | 0.0717 |
| $K_\theta$    | 1.0229 | 1.9209 |
| $K_{\dot{q}}$ | 0.0000 | 0.0000 |

Because the optomotor response is zero if there is no apparent motion to correct for, I do not include an offset in the models. Hence, I do not account for the offset of the individual datapoint from the general mean of the model and as a consequence, the goodness of fit value  $R^2$  loses its meaning. Instead, I calculate the adjusted value  $R_u^2$  which tends to be larger than  $R^2$  (details on are found in appendix C.3). Here,  $R_u^2$  is 0.95, meaning that 95% of the variation in the response behaviour which is caused by changes in frequency is explained by the model  $H_{M,q}(s)$ . The transfer function  $H_{M,q}(s)$  (equation 4.12) is plotted in terms of its magnitude and phase in figure 4.9. This figure illustrates how the control components affect the response behaviour for different frequencies of apparent motion. The blue and red dashed lines in figure 4.9 illustrate the amplitude modulation of the pitch moment response  $M(t)$  due to the proportional and integral feedback of pitch rate, whilst the green dashed line in figure 4.9 illustrates the effect of the time delay on the phase response. The amplitude modulation of  $M(t)$  due to proportional and integral feedback is equal at a frequency of 4 Hz, with the proportional feedback dominating at higher frequencies. The dominating effect of the integral feedback at lower frequencies is reflected by the phase lag which is close to  $-90^\circ$  (see figure 4.7). Imagine if we had the time domain signal of the pitch rate  $q(t)$  and of the pitch angle  $\theta(t)$  with a particular frequency, then we would see that the moment response  $M(t)$  is strongly modulated by  $q(t)$  if the frequency is below 4 Hz, or alternatively,  $M(t)$  is strongly modulated by  $\theta(t)$  at frequencies above 4 Hz.

Next, I repeated this model selection process to find models for the optomotor responses to lateral stimuli. Hence, I fit the family of seven competing models to the magnitude and phase responses of  $L$  or of  $N$  which are generated in response to either  $p$ ,  $r$ ,  $p'$  or  $r'$ . As was already the case for fitting  $H_{M,q}(s)$ , the mean square error is minimised across 14 datapoints. The results of the AICc analysis are shown in table 4.4 and in figures 4.12 and

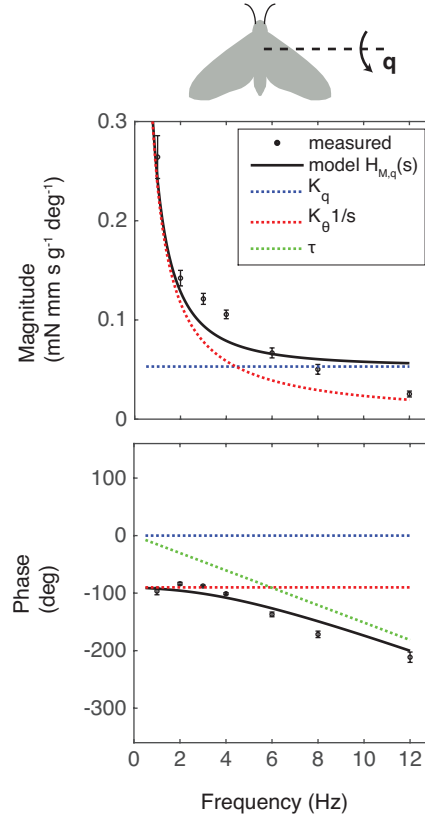


**Figure 4.9:** The measured optomotor responses to pitch rates  $q$  (black, means $\pm$ SEM) are best fitted by  $H_{M,q}(s)$ , a PI-controller with a time delay of 0.042 s (black line). The amplitude modulation of the proportional (blue) and of the integral (red) feedback on the pitch moment response at each frequency is shown in the magnitude (top graph). Below a frequency of 4 Hz, the integral feedback dominates the amplitude modulation of the pitch moment response, whereas above 4 Hz, the proportional feedback dominates the amplitude modulation of the pitch moment response. The time delay (green) only affects the phase roll-off of the responses. Because the integral feedback is dominant at low frequencies, the phase response at 1 Hz is closer to  $-90^\circ$  (rather than being closer to  $0^\circ$  which would indicate the dominance of a proportional feedback at low frequencies).

4.13 (these models are plotted with other models that are going to be fitted to the same data later on in this chapter in order to provide a comparison). The gains  $K_P$ ,  $K_I$ , and  $K_D$  act upon the proportional, integral and derivative feedback of the input  $p$ ,  $r$ ,  $p'$  or  $r'$ . The response moments  $L$  and  $N$  for stimuli  $p$  and  $r'$  are best fitted with either a PI or a PID

controller, i.e. a controller with a combined effect of feedback parameters. The integrator allows the model to capture the magnitude responses at low frequencies and causes the steep decay in the magnitude response as frequency increases (figure 4.12). The combined effect of feedback parameters is reflected by the phase response at low frequencies which is neither at  $0^\circ$  nor  $\pm 90^\circ$  (which is where it would be for the feedback of one parameter only). On the other hand, the response moments  $L$  and  $N$  for stimuli  $r$  and  $p'$  are best fitted by pure proportional controllers. Hence, the magnitude response are fitted by a constant and the phase responses start precisely at  $0^\circ$  or  $180^\circ$  (figure 4.13). This difference in the best performing controller type is a consequence of the different magnitude responses and the weighting of the datapoint with the inverse of the sample variance. Mean datapoints with a small variance are weighted more and are therefore fitted better by the model compared to those datapoints with a large variance and smaller weighting. Hence, the model fits the relatively small magnitude responses to  $r$  and  $p'$  which have a relatively large variance less well than to those responses with a small sample variance, located at higher frequencies. The responses to  $p$  and  $r'$  on the other hand, have a larger magnitude and a smaller variance at low frequencies and therefore, the model has to include an integral that captures that behaviour at low frequencies in order to minimise the mean squared error.

In order to clarify the extent to which the best possible linear control model can explain the optomotor responses to lateral stimuli, I fitted the data with PID-controllers, including a time delay. The PID-controllers improve the fit of the low frequency roll moment responses, i.e.  $H_{L,r}(s)$  and  $H_{L,p'}(s)$  (appendix C.4). But they have the same time delay as the previously fitted P-controllers, and the added integral feedback does not significantly improve the fit for the yaw moment responses, i.e. for  $H_{N,r}(s)$  and  $H_{N,p'}(s)$ . When I set the sample variances equal,  $H_{N,r}(s)$  and  $H_{L,p'}(s)$  are still best fitted by a P-controller

**Table 4.4:** The best control models for the individual transfer functions of the response moments  $L$  or  $N$  for the stimuli  $p$ ,  $r$ ,  $p'$  or  $r'$ .

|            | $H_{L,p}(s)$ | $H_{L,r}(s)$ | $H_{L,p'}(s)$ | $H_{L,r'}(s)$ | $H_{N,p}(s)$ | $H_{N,r}(s)$ | $H_{N,p'}(s)$ | $H_{N,r'}(s)$ |
|------------|--------------|--------------|---------------|---------------|--------------|--------------|---------------|---------------|
| controller | <b>PID</b>   | <b>P</b>     | <b>P</b>      | <b>PI</b>     | <b>PI</b>    | <b>P</b>     | <b>P</b>      | <b>PI</b>     |
| k          | 5            | 3            | 3             | 4             | 4            | 3            | 3             | 4             |
| n          | 14           | 14           | 14            | 14            | 14           | 14           | 14            | 14            |
| $R_u^2$    | 0.98         | 0.52         | 0.16          | 0.69          | 0.80         | 0.86         | 0.66          | 0.65          |
| AICc       | 43.21731     | 49.87794     | 40.74238      | 50.60078      | 35.35202     | 38.89143     | 38.10465      | 30.74118      |
| $\tau$     | 0.007        | 0.077        | 0.037         | 0.047         | 0.029        | 0.057        | 0.061         | 0.053         |
| $K_P$      | -0.0125      | 0.0322       | 0.0164        | 0.0276        | 0.0151       | 0.0378       | -0.0338       | 0.0191        |
| $K_I$      | 1.4181       | 0.0000       | 0.0000        | 0.6324        | -0.2920      | 0.0000       | 0.0000        | -0.3350       |
| $K_D$      | 0.0003       | 0.0000       | 0.0000        | 0.0000        | 0.0000       | 0.0000       | 0.0000        | 0.0000        |

because their magnitude responses are flat and their phase responses lie around  $0^\circ$  at low frequencies. On the other hand,  $H_{L,r}(s)$  and  $H_{N,p'}(s)$  change to be fitted best by PI-controllers instead of P-controllers. Hence, the weighting of the mean square error with the inverse of the sample variance significantly affects the AICc model selection process.

Based on these findings I am confident that linear control models and the model fitting process are a sensible way of capturing the optomotor response behaviour for both longitudinal and lateral stimuli. Using these individual control models I can now explore spatial superposition with two different approaches. First, in section 4.4, I linearly superpose the effect of individual controllers to predict the controllers used in response to  $p''$ . Second, in section 4.5, I lump the responses to the lateral stimuli and explore if a more parsimonious controller is able to explain the variation in response dynamics, despite the variation in stimulus axis. Hence, is there a control model with a fixed set of gains and time delay that explains the variation in the optomotor responses for a large set of stimulus axis?

## 4.4 Testing spatial superposition of the responses to stimuli that combine lateral and longitudinal motion

In this section I discuss how predictable the responses to stimuli  $p''$  are under the assumption of spatial superposition. The rationale behind the principle of spatial superposition is the following: Because the stimulus axis for  $p''$  lies at  $45^\circ$  intermediate to the stimulus axis for  $p$  and  $q$ , the control laws that are used to stabilise  $p$  and  $q$  contribute to equal amounts in stabilising  $p''$ .

$$p'' = \cos(45^\circ)p + \cos(45^\circ)q$$

Hence, the responses to  $p''$  should correspond to the projections of the responses to  $p$  and  $q$  onto the intermediate axis (figure 4.10). In order to test this, I take the previously fitted control models  $H_{L,p}(s)$ ,  $H_{N,p}(s)$  and  $H_{M,q}(s)$  that explain the responses to  $p$  and  $q$  and multiply them with  $\cos(45^\circ)$  in order to predict the responses to  $p''$ , i.e.  $H_{L,p''}(s)$ ,  $H_{M,p''}(s)$  and  $H_{N,p''}(s)$ :

$$H_{L,p''}(s) = \cos(45^\circ) \cdot H_{L,p}(s)$$

$$H_{M,p''}(s) = \cos(45^\circ) \cdot H_{M,q}(s)$$

$$H_{N,p''}(s) = \cos(45^\circ) \cdot H_{N,p}(s)$$

The 95% confidence intervals for  $H_{L,p}(s)$  and  $H_{N,p}(s)$  are given in table 4.5.

The predicted frequency responses to  $p''$  and their corresponding confidence intervals

**Table 4.5:** 95% confidence intervals of the feedback gains for the PID-controller  $H_{L,p}(s)$  and for the PI-controller  $H_{N,p}(s)$ . These confidence intervals are taken into account in the prediction of the responses to  $p''$ .

|               | $H_{L,p}(s)$ |         | $H_{N,p}(s)$ |         |
|---------------|--------------|---------|--------------|---------|
| $K_p$         | -0.0183      | -0.0068 | 0.0104       | 0.0198  |
| $K_\phi$      | 1.1188       | 1.7173  | -0.4122      | -0.1719 |
| $K_{\dot{p}}$ | 0.0002       | 0.0005  | 0            | 0       |

are illustrated in figure 4.10. The phase difference of  $\sim 180^\circ$  in the pitch response moment  $M$  to  $q$  and  $p''$  is due to the difference in the stimulus direction ( $q$  starts with a nose-up motion whereas  $p''$  starts with a nose-down motion). I treat the responses to  $q$  as if it were the responses to  $-q$  because on grounds of body symmetry I expect the moth to produce the same magnitude response to  $q$  and to  $-q$ , only with a phase shift of  $180^\circ$ .

Within the 95% confidence intervals (shaded areas in figure 4.10), the linear spatial superposition predicts the roll and pitch magnitude responses to  $p''$  quite well, especially for frequencies  $\geq 6$  Hz. If I approximate the confidence interval of the measured responses to  $p''$  as double the error bar, then the phase responses for frequencies  $< 6$  Hz are well captured by the prediction. Qualitatively, the spatial superposition predicts the magnitude and phase responses relatively well before the phase responses become non-linear.

I conclude that spatial superposition of optic flow fields that combine longitudinal and lateral motion is met for frequencies  $< 6$  Hz. Although the magnitude responses are well predicted for frequencies  $\geq 6$  Hz, the phase responses to  $p''$  for those higher frequencies suggest non-linearities which cannot be explained by a linear superposition. This could indicate that the different time delays of the PI-controllers and their effect on the phase roll-off may be more pronounced at frequencies  $\geq 6$  Hz.

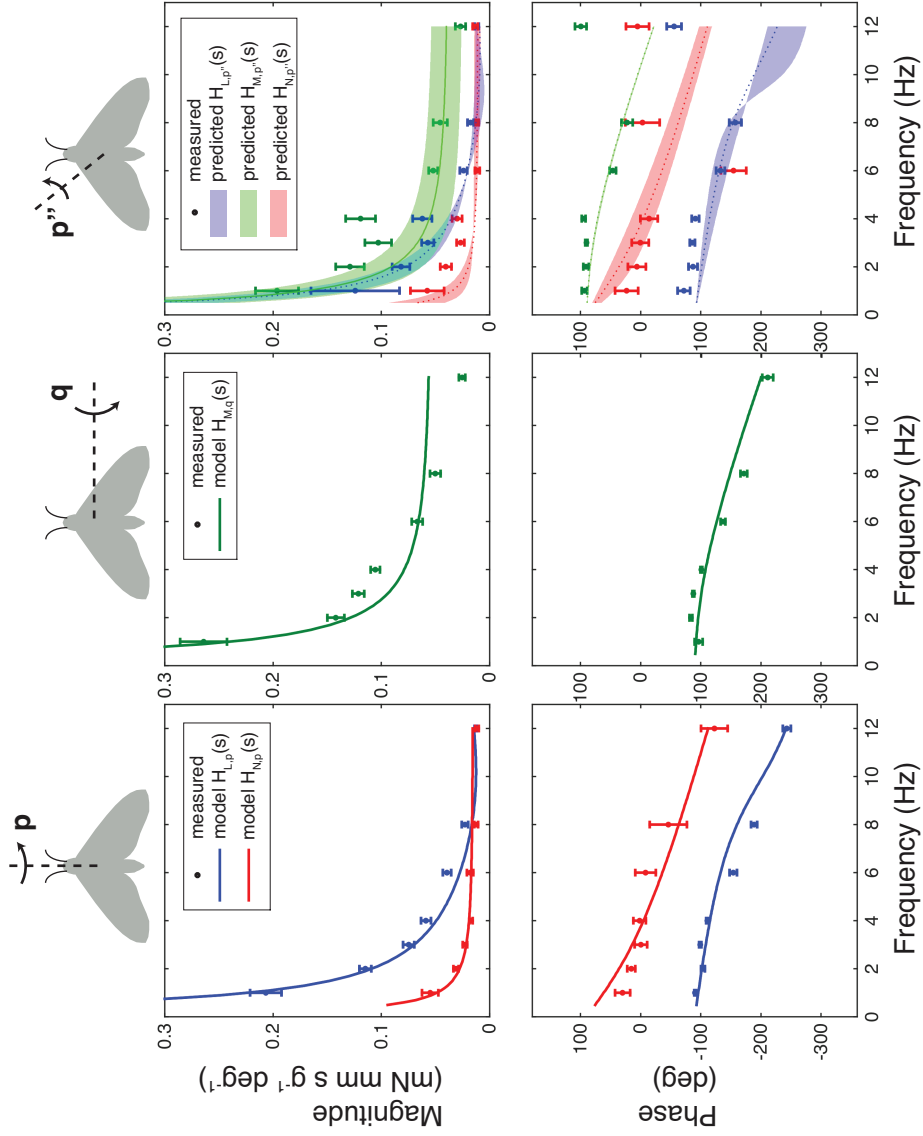


**Figure 4.10:** Spatial superposition is tested by rescaling the modelled responses to  $p$  (left column) and  $q$  (middle column) to predict the responses to  $p''$  (right column). The top row illustrates the measured (means of the individual means $\pm$ SEM) and modelled (full line) magnitude responses. The bottom row illustrates the measured and modelled phase responses. The shaded areas in the last column indicate the 95% confidence interval of the predicted roll (blue), pitch (green) and yaw (red) moment responses to  $p''$ .

## 4.5 Testing spatial superposition of the responses to lateral stimuli

In the previous section I fitted control models to the individual response moments  $L$ ,  $M$  and  $N$  which helped understand the model fitting process and which has also proven sufficient to derive the control laws for a single-input, single-output system such as  $H_{M,q}(s)$ . But the coupled responses to lateral stimuli represent a multiple-output system and it is therefore more appropriate to fit a model to the combined roll and yaw response moments for a particular stimulus. I further expand this approach to a multiple-input, multiple-output system in order to address spatial superposition. Hence, I group the responses to multiple types of lateral stimuli and ask whether there is a control model with a fixed set of gains and a time delay that explains the variation in the optomotor responses for an expanded set of lateral stimuli.

As previously mentioned, stimuli  $p$  and  $r'$  lead to relatively large magnitude responses and are fitted by PI- or PID-controllers. In contrast, the stimuli  $r$  and  $p'$  lead to relatively low magnitude responses and tend to be fitted by pure P-controllers. Based on this, I lump the optomotor responses into two groups (figure 4.11): The first group comprises the roll and yaw response moments to  $p$  and  $r'$ . These dynamics are fitted by the multi-input, multi-output transfer function matrix  $H_1(s)$ . The second group comprises the roll and yaw response moments to  $r$  and  $p'$ . These dynamics are fitted by the multi-input, multi-output transfer function matrix  $H_2(s)$ . Here I am fitting a transfer function matrix that contains four transfer functions. The four functions describe the transform of  $p$  to  $L$ ,  $p$  to  $N$ ,  $r$  to  $L$  and  $r$  to  $N$ .

The control outputs are defined as the roll response  $L$  and the yaw response  $N$ . For ease of comparison across the different models, I define the input as the angular rates

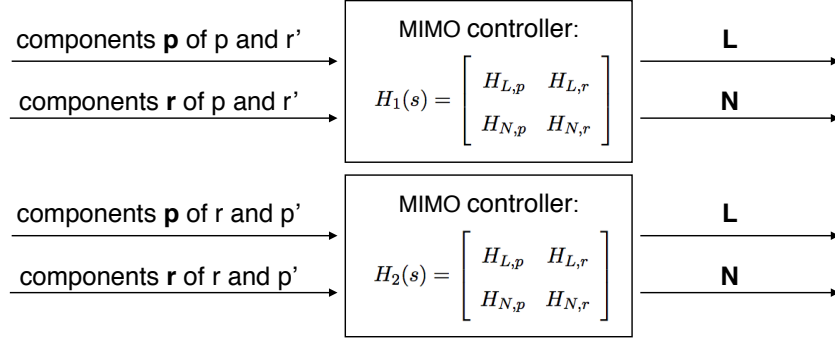


**Figure 4.11:** The transfer function  $H_1(s)$  is a  $2 \times 2$  matrix that describes the dynamic relationship between the response moments  $L$  and  $N$  and the two types of stimuli  $p$  and  $r'$ . The transfer function  $H_2(s)$  is a  $2 \times 2$  matrix that describes the dynamic relationship between the response moments  $L$  and  $N$  and the two types of stimuli  $r$  and  $p'$ . For the model fitting process, the visual stimuli are expressed as motion components along the x- and the z-axis, i.e. the corresponding roll rate  $p$  and the yaw rate  $r$ . Therefore, each response moment is expressed as a function of six gains:  $K_{out,p}$ ,  $K_{out,\phi}$ , and  $K_{out,\dot{p}}$  are the proportional, integral, and derivative gains on the motion perceived along the x-axis;  $K_{out,r}$ ,  $K_{out,\psi}$ , and  $K_{out,\dot{r}}$  are the proportional, integral, and derivative gains on the motion perceived along the z-axis. The subscript *out* shows that there is a set of six gains for the roll moment response  $L$  and a set of six gains for the yaw moment response  $N$ . Each of the four components of  $H_1(s)$  or  $H_2(s)$  describe the dynamic relationship between one moment output and one stimulus input only.

$p$  and  $r$ , i.e. the angular rate along the axes of the control outputs  $L$  and  $N$ . Hence, I express the visual stimuli  $p$ ,  $r$ ,  $p'$ , and  $r'$  with their corresponding components along the x- and the z-axis (table 4.6). It is highly likely that the moths rely on more than two visual input axes in order to generate their response moments, but for this model fitting, a third input axis would lead to rank deficiency in the predictor matrix  $\mathbf{x}$  and as a consequence, the parameter estimates would be unidentifiable. I use the factors in table 4.6 in order to define the correct parameters along the x- and z-axis for the four different types of stimuli. For instance, the optic flow along an axis orthogonal to the stimulus axis is set to zero whereas the optic flow along an axis at  $45^\circ$  to the stimulus axis is weighted by  $\frac{1}{\sqrt{2}}$ .

**Table 4.6:** The weighting factors of the components in the predictor matrix  $\mathbf{x}$  are either 0, 1,  $\frac{1}{\sqrt{2}}$  or  $-\frac{1}{\sqrt{2}}$  and depend on the stimulus being either  $p$ ,  $r$ ,  $p'$  or  $r'$ .

| stimulus | motion perceived along the x-axis | motion perceived along the z-axis |
|----------|-----------------------------------|-----------------------------------|
| $p$      | 1                                 | 0                                 |
| $r'$     | $\frac{1}{\sqrt{2}}$              | $\frac{1}{\sqrt{2}}$              |
| $r$      | 0                                 | 1                                 |
| $p'$     | $-\frac{1}{\sqrt{2}}$             | $-\frac{1}{\sqrt{2}}$             |

The first three columns of the predictor matrix  $\mathbf{x}$  in equations 4.13 and 4.14 correspond to the visual parameters perceived along the x-axis. The latter three columns of the predictor matrix  $\mathbf{x}$  correspond to the visual parameters perceived along the z-axis. The 14 rows of the predictor matrix  $\mathbf{x}$  represent the input for the two types of stimuli, each of which was presented with seven different frequencies  $s_1$  to  $s_7$  (see equation 4.10). Hence, when I solve  $\mathbf{Y}_L = \mathbf{xK}$  and  $\mathbf{Y}_N = \mathbf{xK}$ , each response moment  $out = L$  or  $N$  is expressed as a function of six gains:  $K_{out,p}$ ,  $K_{out,\phi}$ , and  $K_{out,\dot{p}}$  which are the proportional, integral, and derivative gains on the motion perceived along the x-axis; and  $K_{out,r}$ ,  $K_{out,\psi}$ , and  $K_{out,\dot{r}}$  which are the proportional, integral, and derivative gains on the motion perceived along the z-axis. I apply the AICc analysis to each group under the assumption that  $L$  and  $N$  are generated with the same time delay  $\tau$ . Hence, the mean square error is now minimised for the lumped roll and yaw moment responses generated in response to the two lateral stimuli of the corresponding group, hereby quadrupling the fitted dataset to 56 points. Each of the four controllers in  $H_1(s)$  or  $H_2(s)$  will have the same time delay, but different gains, because each controller describes the control of a particular moment response in function of the visual parameters provided along a particular input axis.

$$\mathbf{x}_{p,r'}\mathbf{K} = \left\{ \begin{array}{l} p \\ r' \end{array} \right\} \left[ \begin{array}{cccccc} e^{-s_1\tau} & \frac{1}{s_1}e^{-s_1\tau} & s_1e^{-s_1\tau} & 0 & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ e^{-s_7\tau} & \frac{1}{s_7}e^{-s_7\tau} & s_7e^{-s_7\tau} & 0 & 0 & 0 \\ \frac{1}{\sqrt{2}}e^{-s_1\tau} & \frac{1}{\sqrt{2}}\frac{1}{s_1}e^{-s_1\tau} & \frac{1}{\sqrt{2}}s_1e^{-s_1\tau} & \frac{1}{\sqrt{2}}e^{-s_1\tau} & \frac{1}{\sqrt{2}}\frac{1}{s_1}e^{-s_1\tau} & \frac{1}{\sqrt{2}}s_1e^{-s_1\tau} \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ \frac{1}{\sqrt{2}}e^{-s_7\tau} & \frac{1}{\sqrt{2}}\frac{1}{s_7}e^{-s_7\tau} & \frac{1}{\sqrt{2}}s_7e^{-s_7\tau} & \frac{1}{\sqrt{2}}e^{-s_7\tau} & \frac{1}{\sqrt{2}}\frac{1}{s_7}e^{-s_7\tau} & \frac{1}{\sqrt{2}}s_7e^{-s_7\tau} \end{array} \right] \left[ \begin{array}{c} K_{out,p} \\ K_{out,\phi} \\ K_{out,\dot{p}} \\ K_{out,r} \\ K_{out,\psi} \\ K_{out,\dot{r}} \end{array} \right] \quad (4.13)$$

$$\mathbf{x}_{r,p'}\mathbf{K} = \left\{ \begin{array}{l} r \\ p' \end{array} \right\} \left[ \begin{array}{cccccc} 0 & 0 & 0 & e^{-s_1\tau} & \frac{1}{s_1}e^{-s_1\tau} & s_1e^{-s_1\tau} \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & e^{-s_7\tau} & \frac{1}{s_7}e^{-s_7\tau} & s_7e^{-s_7\tau} \\ \frac{1}{\sqrt{2}}e^{-s_1\tau} & \frac{1}{\sqrt{2}}\frac{1}{s_1}e^{-s_1\tau} & \frac{1}{\sqrt{2}}s_1e^{-s_1\tau} & -\frac{1}{\sqrt{2}}e^{-s_1\tau} & -\frac{1}{\sqrt{2}}\frac{1}{s_1}e^{-s_1\tau} & -\frac{1}{\sqrt{2}}s_1e^{-s_1\tau} \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ \frac{1}{\sqrt{2}}e^{-s_7\tau} & \frac{1}{\sqrt{2}}\frac{1}{s_7}e^{-s_7\tau} & \frac{1}{\sqrt{2}}s_7e^{-s_7\tau} & -\frac{1}{\sqrt{2}}e^{-s_7\tau} & -\frac{1}{\sqrt{2}}\frac{1}{s_7}e^{-s_7\tau} & -\frac{1}{\sqrt{2}}s_7e^{-s_7\tau} \end{array} \right] \left[ \begin{array}{c} K_{out,p} \\ K_{out,\phi} \\ K_{out,\dot{p}} \\ K_{out,r} \\ K_{out,\psi} \\ K_{out,\dot{r}} \end{array} \right] \quad (4.14)$$

Table 4.7 shows the AICc analysis for the lumped responses to  $p$  and  $r'$ , i.e. for  $H_1(s)$ . The multi-input, multi-output transfer function matrix  $H_1(s)$  consists of four PI-controllers with a time delay of 0.047 s.

The 95% confidence intervals of the control gains of  $H_1(s)$  are given in table 4.8.

The four individual transfer functions that comprise  $H_1(s)$  are given in equations 4.16 to 4.19 and are plotted in figure 4.12.

**Table 4.7:** Result of the AICc analysis for the lumped roll and yaw moments  $L$  and  $N$ , generated in response to stimuli  $p$  and  $r'$ . The multi-input, multi-output transfer function matrix  $H_1(s)$  consists of four PI-controllers with a time delay of 0.047 s.

|                 | PID       | PD        | PI       | ID        | P        | D         | I        |
|-----------------|-----------|-----------|----------|-----------|----------|-----------|----------|
| k               | 14        | 10        | 10       | 10        | 6        | 6         | 6        |
| n               | 56        | 56        | 56       | 56        | 56       | 56        | 56       |
| AICc            | 167.9708  | 217.3179  | 159.2036 | 199.7686  | 215.4052 | 225.27    | 196.2681 |
| Lh              | 0.01248   | 2.40E-13  | 1        | 1.55E-09  | 6.25E-13 | 4.51E-15  | 8.94E-09 |
| $\tau$          | 0.045     | 0.043     | 0.047    | 0.029     | 0.055    | 0.033     | 0.028    |
| $K_{L,p}$       | 0.017282  | 0.008231  | 0.018066 | 0         | 0.016335 | 0         | 0        |
| $K_{L,\phi}$    | 0.978793  | 0         | 0.874556 | 1.114185  | 0        | 0         | 1.09832  |
| $K_{L,\dot{p}}$ | 4.56E-05  | -2.28E-04 | 0        | 1.94E-05  | 0        | -2.71E-04 | 0        |
| $\bar{K}_{L,r}$ | 0.019784  | 0.020955  | 0.020997 | 0         | 0.021978 | 0         | 0        |
| $K_{L,\psi}$    | -0.03973  | 0         | 0.018531 | -0.03243  | 0        | 0         | 0.273687 |
| $K_{L,\dot{r}}$ | -9.69E-05 | -0.00017  | 0        | -0.00023  | 0        | -0.00026  | 0        |
| $\bar{K}_{N,p}$ | 0.008316  | 0.011424  | 0.007202 | 0         | 0.008114 | 0         | 0        |
| $K_{N,\phi}$    | -0.3462   | 0         | -0.3953  | -0.37933  | 0        | 0         | -0.34321 |
| $K_{N,\dot{p}}$ | 8.67E-05  | 0.000283  | 0        | -6.36E-05 | 0        | 0.000191  | 0        |
| $\bar{K}_{N,r}$ | 0.021497  | 0.020524  | 0.024548 | 0         | 0.017345 | 0         | 0        |
| $K_{N,\psi}$    | -0.08159  | 0         | 0.081864 | 0.000707  | 0        | 0         | 0.35081  |
| $K_{N,\dot{r}}$ | -0.00026  | -0.00039  | 0        | -0.00034  | 0        | -0.00042  | 0        |

**Table 4.8:** The 95% confidence intervals for the control gains of  $H_1(s)$ .

|                 |         |         |
|-----------------|---------|---------|
| $K_{L,p}$       | 0.0106  | 0.0255  |
| $K_{L,\phi}$    | 0.6631  | 1.0860  |
| $K_{L,\dot{p}}$ | 0       | 0       |
| $\bar{K}_{L,r}$ | 0.0061  | 0.0359  |
| $K_{L,\psi}$    | -0.4238 | 0.4608  |
| $K_{L,\dot{r}}$ | 0       | 0       |
| $\bar{K}_{N,p}$ | 0.0005  | 0.0139  |
| $K_{N,\phi}$    | -0.5469 | -0.2437 |
| $K_{N,\dot{p}}$ | 0       | 0       |
| $\bar{K}_{N,r}$ | 0.0111  | 0.0380  |
| $K_{N,\psi}$    | -0.2757 | 0.4395  |
| $K_{N,\dot{r}}$ | 0       | 0       |

$$H_1(s) = \begin{bmatrix} H_{L,p} & H_{L,r} \\ H_{N,p} & H_{N,r} \end{bmatrix} \quad (4.15)$$

$$H_{L,p}(s) = \left( 0.018 + 0.874 \frac{1}{s} \right) e^{-s0.047} \quad (4.16)$$

$$H_{L,r}(s) = \left( 0.021 + 0.019 \frac{1}{s} \right) e^{-s0.047} \quad (4.17)$$

$$H_{N,p}(s) = \left( 0.007 - 0.395 \frac{1}{s} \right) e^{-s0.047} \quad (4.18)$$

$$H_{N,r}(s) = \left( 0.025 + 0.082 \frac{1}{s} \right) e^{-s0.047} \quad (4.19)$$

Table 4.9 shows the AICc analysis for the lumped responses to  $r$  and  $p'$ , i.e. for  $H_2(s)$ . The multi-input, multi-output transfer function matrix  $H_2(s)$  consists of four PI-controllers with a time delay of 0.060 s.

The 95% confidence intervals of the control gains of  $H_2(s)$  are given in table 4.10.

The four individual transfer functions that comprise  $H_2(s)$  are given in equations 4.21 to 4.24 and are plotted in figure 4.13.

$$H_2(s) = \begin{bmatrix} H_{L,p} & H_{L,r} \\ H_{N,p} & H_{N,r} \end{bmatrix} \quad (4.20)$$

**Table 4.9:** Result of the AICc analysis for the lumped roll and yaw moments  $L$  and  $N$ , generated in response to stimuli  $r$  and  $p'$ . The multi-input, multi-output transfer function matrix  $H_2(s)$  consists of four PI-controllers with a time delay of 0.060 s.

|                 | PID      | PD       | PI       | ID       | P        | D        | I        |
|-----------------|----------|----------|----------|----------|----------|----------|----------|
| k               | 14       | 10       | 10       | 10       | 6        | 6        | 6        |
| n               | 56       | 56       | 56       | 56       | 56       | 56       | 56       |
| AICc            | 178.3434 | 176.5439 | 172.0165 | 227.428  | 189.6925 | 226.1048 | 232.1302 |
| Lh              | 0.042281 | 0.103966 | 1        | 9.28E-13 | 0.000145 | 1.80E-12 | 8.84E-14 |
| $\tau$          | 0.063    | 0.064    | 0.060    | 0.000    | 0.059    | 0.081    | 0.020    |
| $K_{L,p}$       | 0.0308   | 0.0296   | 0.0335   | 0.0000   | 0.0344   | 0.0000   | 0.0000   |
| $K_{L,\phi}$    | -0.2939  | 0.0000   | -0.4058  | 1.6000   | 0.0000   | 0.0000   | 1.2093   |
| $K_{L,\dot{p}}$ | 0.0000   | 0.0000   | 0.0000   | 0.0004   | 0.0000   | 0.0004   | 0.0000   |
| $\bar{K}_{L,r}$ | 0.0248   | 0.0241   | 0.0229   | 0.0000   | 0.0186   | 0.0000   | 0.0000   |
| $K_{L,\psi}$    | 0.3024   | 0.0000   | 0.4483   | 1.0289   | 0.0000   | 0.0000   | 0.6931   |
| $K_{L,\dot{r}}$ | -0.0002  | -0.0003  | 0.0000   | 0.0004   | 0.0000   | 0.0001   | 0.0000   |
| $\bar{K}_{N,p}$ | -0.0119  | -0.0120  | -0.0109  | 0.0000   | -0.0092  | 0.0000   | 0.0000   |
| $K_{N,\phi}$    | -0.0622  | 0.0000   | -0.1481  | -0.8486  | 0.0000   | 0.0000   | -0.4601  |
| $K_{N,\dot{p}}$ | 0.0001   | 0.0001   | 0.0000   | -0.0001  | 0.0000   | -0.0001  | 0.0000   |
| $\bar{K}_{N,r}$ | 0.0359   | 0.0354   | 0.0369   | 0.0000   | 0.0371   | 0.0000   | 0.0000   |
| $K_{N,\psi}$    | -0.0253  | 0.0000   | -0.0418  | 0.6118   | 0.0000   | 0.0000   | 0.4075   |
| $K_{N,\dot{r}}$ | 0.0002   | 0.0002   | 0.0000   | 0.0004   | 0.0000   | 0.0005   | 0.0000   |

**Table 4.10:** The 95% confidence intervals for the control gains of  $H_2(s)$ .

|                 |         |        |
|-----------------|---------|--------|
| $K_{L,p}$       | 0.0171  | 0.0499 |
| $K_{L,\phi}$    | -0.8813 | 0.0698 |
| $K_{L,\dot{p}}$ | 0       | 0      |
| $\bar{K}_{L,r}$ | 0.0137  | 0.0321 |
| $K_{L,\psi}$    | 0.2142  | 0.6825 |
| $K_{L,\dot{r}}$ | 0       | 0      |
| $\bar{K}_{N,p}$ | -0.0298 | 0.0079 |
| $K_{N,\phi}$    | -0.6216 | 0.3255 |
| $K_{N,\dot{p}}$ | 0       | 0      |
| $\bar{K}_{N,r}$ | 0.0292  | 0.0446 |
| $K_{N,\psi}$    | -0.2277 | 0.1441 |
| $K_{N,\dot{r}}$ | 0       | 0      |

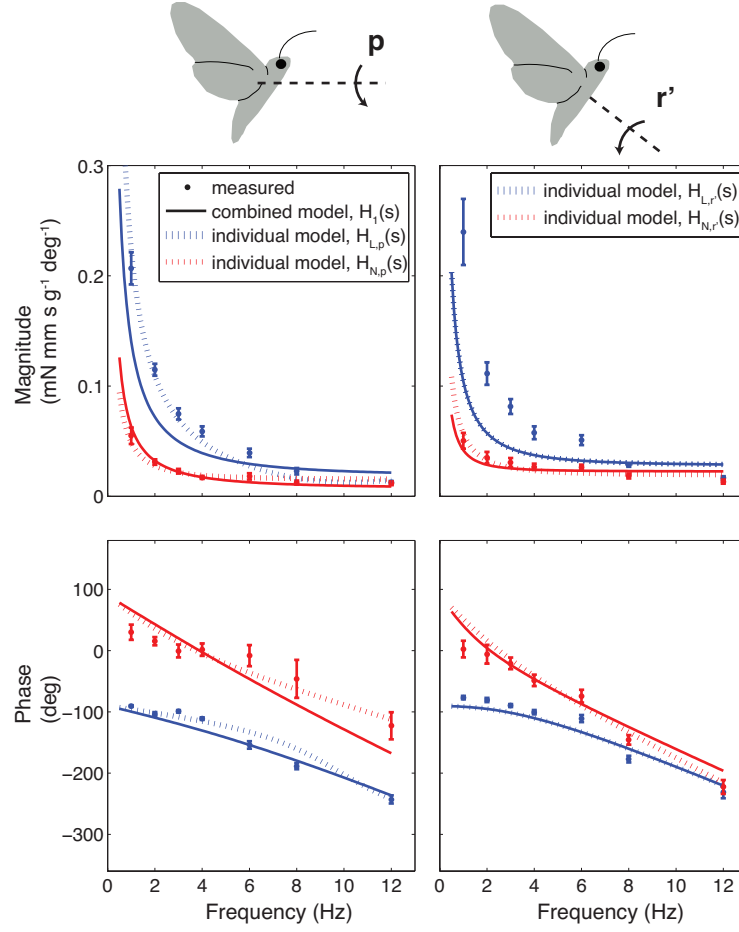


**Figure 4.12:** The measured (mean of mean individuals  $\pm$ SEM) and modelled frequency responses to stimuli  $p$  (left column) and  $r'$  (right column). The colours indicate the roll (blue) and the yaw (red) response moments. The dashed lines illustrate the models fitted to the individual response moments ( $n=14$ , table 4.4). The full lines illustrate the PI-controllers in  $H_1(s)$  which have been fitted to the lumped dataset ( $n=56$ , table 4.7).

$$H_{L,p}(s) = \left(0.034 - 0.406\frac{1}{s}\right) e^{-s0.060} \quad (4.21)$$

$$H_{L,r}(s) = \left(0.023 + 0.448\frac{1}{s}\right) e^{-s0.060} \quad (4.22)$$

$$H_{N,p}(s) = \left(-0.011 - 0.148\frac{1}{s}\right) e^{-s0.060} \quad (4.23)$$

$$H_{N,r}(s) = \left(0.037 - 0.042\frac{1}{s}\right) e^{-s0.060} \quad (4.24)$$

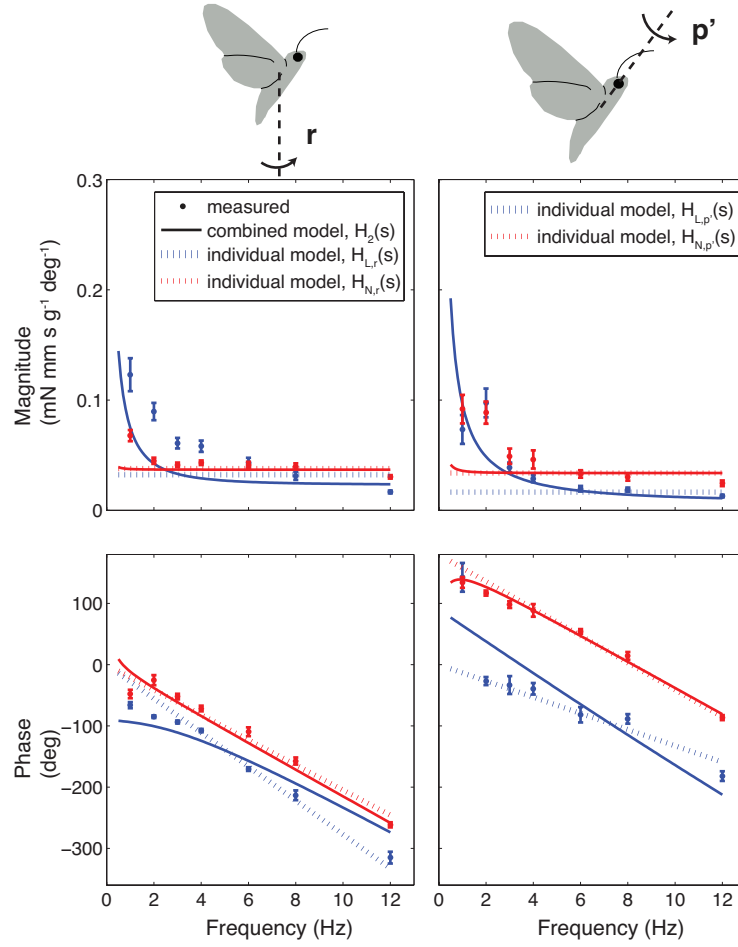


**Figure 4.13:** The measured (mean of individual means  $\pm$ SEM) and modelled frequency responses to stimuli  $r$  (left column) and  $p'$  (right column). The colours indicate the roll (blue) and the yaw (red) response moments. The dashed lines illustrate the models fitted to the individual response moments ( $n=14$ , table 4.4). The full lines illustrate the PI-controllers in  $H_2(s)$  which have been fitted to the lumped dataset ( $n=56$ , table 4.9).

The AICc analysis delivers a set of four PI-controllers as the best fitting models for  $H_1(s)$  and  $H_2(s)$ . For both models I find that the phase responses are well fitted in comparison to the magnitude responses. The magnitude responses contain larger variability which is potentially caused by the individual's motivation or fitness. The timing of the response on the other hand, contains less intrinsic variability. The two transfer function matrices  $H_1(s)$  and  $H_2(s)$  have control gains that significantly differ in their magnitude and also

in their sign. Also, the time delays of the seven competing models fitted to the responses to  $r$  and  $p'$  (table 4.9) are on average larger than those fitted to  $p$  and  $r'$  (table 4.7). The time delay determines the steepness of the phase roll-off and subsequently affects the fitted control gains. The average phase roll-off for the responses to  $r$  and  $p'$  is steeper by  $62^\circ$  over 11 Hz, i.e.  $6^\circ/\text{Hz}$  when compared to the phase roll-off for stimuli  $p$  and  $r'$ . This difference corresponds to an average difference in delay of 0.016 s. A steeper phase roll-off indicates a larger time delay of the system, which is what the model fitting process delivers for the controllers in  $H_2(s)$ .

The roll magnitude responses dominate the responses to low frequency stimuli  $p$  and  $r'$ . In contrast, the roll and yaw magnitude responses to stimuli  $r$  and  $p'$  have a similar magnitude. A response that contains a larger yaw magnitude response may be slower because of the larger passive damping provided for motion about the vertical axis [64]. As I will discuss in the next chapter, a disturbance about the yaw axis does not threaten the inherent instability of the moth and therefore, yaw motion may not be prioritised for a fast control response.

### **4.5.1 Fitting a global model to the responses to all lateral stimuli**

In this last section, I test the performance of the most parsimonious control model. Hence, I test how well a global model explains the variation in the responses to lateral stimuli which is caused by temporal frequency, moment response and stimulus axis. If the principle of spatial superposition holds for lateral stimuli, this global model should predict all response behaviours for the four types of lateral stimuli. Hence, I could use this control model to predict the response behaviour for a stimulus about an arbitrary axis within the mid-sagittal plane. A linearisable response behaviour could also indicate that the information across different visual axes is equally weighted and linearly superposed to

generate the necessary control output.

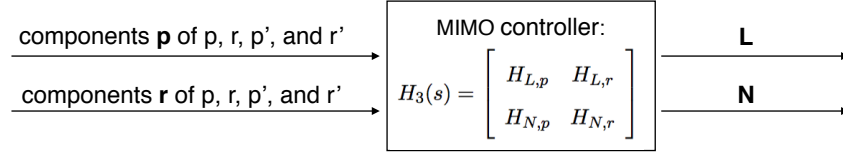


**Figure 4.14:** The transfer function  $H_3(s)$  is a  $2 \times 2$  matrix that describes the dynamic relationship between the response moments  $L$  and  $N$  and the four types of stimuli  $p$ ,  $r$ ,  $p'$ , and  $r'$ . For the model fitting process, the visual stimuli are expressed as motion components along the x- and the z-axis, i.e. the roll rate  $p$  and the yaw rate  $r$ . Therefore, each response moment is expressed as a function of six gains:  $K_{out,p}$ ,  $K_{out,\phi}$ , and  $K_{out,\dot{p}}$  are the proportional, integral, and derivative gains on the motion perceived along the x-axis;  $K_{out,r}$ ,  $K_{out,\psi}$ , and  $K_{out,\dot{r}}$  are the proportional, integral, and derivative gains on the motion perceived along the z-axis. Each component of  $H_3(s)$  describes the dynamic relationship between one moment output and one stimulus input only.

As shown in equation 4.25, the predictor matrix  $\mathbf{x}$  has six columns in order to describe the apparent ego-motion provided by  $p$ ,  $r$ ,  $p'$  and  $r'$  along the x- and the z-axis. The six columns contain the predictors for the six control gains in  $\mathbf{K}$ . I pool all 112 datapoints, i.e. the mean magnitude and phase of the roll and yaw response moments for the seven frequencies and four stimulus axes, and fit the family of seven candidate models. I still assume the same time delay  $\tau$  for both response moments  $L$  and  $N$ .

$$\mathbf{xK} = \left\{ \begin{array}{l} p \\ r \\ p' \\ r' \end{array} \right\} \left[ \begin{array}{cccccc} e^{-s_1\tau} & \frac{1}{s_1}e^{-s_1\tau} & s_1e^{-s_1\tau} & 0 & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ e^{-s_7\tau} & \frac{1}{s_7}e^{-s_7\tau} & s_7e^{-s_7\tau} & 0 & 0 & 0 \\ 0 & 0 & 0 & e^{-s_1\tau} & \frac{1}{s_1}e^{-s_1\tau} & s_1e^{-s_1\tau} \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & e^{-s_7\tau} & \frac{1}{s_7}e^{-s_7\tau} & s_7e^{-s_7\tau} \\ \frac{1}{\sqrt{2}}e^{-s_1\tau} & \frac{1}{\sqrt{2}}\frac{1}{s_1}e^{-s_1\tau} & \frac{1}{\sqrt{2}}s_1e^{-s_1\tau} & -\frac{1}{\sqrt{2}}e^{-s_1\tau} & -\frac{1}{\sqrt{2}}\frac{1}{s_1}e^{-s_1\tau} & -\frac{1}{\sqrt{2}}s_1e^{-s_1\tau} \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ \frac{1}{\sqrt{2}}e^{-s_7\tau} & \frac{1}{\sqrt{2}}\frac{1}{s_7}e^{-s_7\tau} & \frac{1}{\sqrt{2}}s_7e^{-s_7\tau} & -\frac{1}{\sqrt{2}}e^{-s_7\tau} & -\frac{1}{\sqrt{2}}\frac{1}{s_7}e^{-s_7\tau} & -\frac{1}{\sqrt{2}}s_7e^{-s_7\tau} \\ \frac{1}{\sqrt{2}}e^{-s_1\tau} & \frac{1}{\sqrt{2}}\frac{1}{s_1}e^{-s_1\tau} & \frac{1}{\sqrt{2}}s_1e^{-s_1\tau} & \frac{1}{\sqrt{2}}e^{-s_1\tau} & \frac{1}{\sqrt{2}}\frac{1}{s_1}e^{-s_1\tau} & \frac{1}{\sqrt{2}}s_1e^{-s_1\tau} \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ \frac{1}{\sqrt{2}}e^{-s_7\tau} & \frac{1}{\sqrt{2}}\frac{1}{s_7}e^{-s_7\tau} & \frac{1}{\sqrt{2}}s_7e^{-s_7\tau} & \frac{1}{\sqrt{2}}e^{-s_7\tau} & \frac{1}{\sqrt{2}}\frac{1}{s_7}e^{-s_7\tau} & \frac{1}{\sqrt{2}}s_7e^{-s_7\tau} \end{array} \right] \left[ \begin{array}{c} K_{out,p} \\ K_{out,\phi} \\ K_{out,\dot{p}} \\ K_{out,r} \\ K_{out,\psi} \\ K_{out,\dot{r}} \end{array} \right] \quad (4.25)$$

The AICc analysis for this 2-input, 2-output system is shown in table 4.11. The PID-controller with a time delay of 0.052 s performs best in fitting the lumped roll and yaw response moments for stimuli  $p$ ,  $r$ ,  $p'$  and  $r'$ . The 95% confidence intervals for the control gains are presented in table 4.12. In contrast to the PI-controllers which were fitted in previous section, these controllers suggest that the derivative function of the input is also necessary to provide a control output. Although, the confidence interval of all four derivative gains  $K_{L,\dot{p}}$ ,  $K_{N,\dot{p}}$ ,  $K_{L,\dot{r}}$ , and  $K_{N,\dot{r}}$  include zero and hereby indicate that the derivative function does not have a significant effect. Figure 4.15 illustrates how well the four components of the transfer function matrix  $H_3(s)$  in equations 4.27 to 4.30 perform across the parameter range of the stimuli.

**Table 4.11:** Result of the AICc analysis for the lumped roll and yaw moments  $L$  and  $N$  (112 datapoints), generated in response to lateral stimuli  $p$ ,  $r$ ,  $p'$ , and  $r'$ . The multi-input, multi-output transfer function matrix  $H_3(s)$  consists of four PID-controllers with a time delay of 0.052 s.

|                 | PID      | PD       | PI       | ID       | P        | D        | I        |
|-----------------|----------|----------|----------|----------|----------|----------|----------|
| k               | 14       | 10       | 10       | 10       | 6        | 6        | 6        |
| n               | 112      | 112      | 112      | 112      | 112      | 112      | 112      |
| AICc            | 342.0605 | 388.1786 | 347.886  | 415.5808 | 401.2592 | 440.8857 | 421.1789 |
| Lh              | 1        | 9.67E-11 | 0.054326 | 1.08E-16 | 1.40E-13 | 3.47E-22 | 6.60E-18 |
| $\tau$          | 0.052    | 0.055    | 0.053    | 0.030    | 0.059    | 0.036    | 0.025    |
| $K_{L,p}$       | 0.0245   | 0.0203   | 0.0245   | 0.0000   | 0.0211   | 0.0000   | 0.0000   |
| $K_{L,\phi}$    | 0.6706   | 0.0000   | 0.4888   | 0.8329   | 0.0000   | 0.0000   | 1.0444   |
| $K_{L,\dot{p}}$ | 0.0001   | 0.0000   | 0.0000   | -0.0001  | 0.0000   | -0.0003  | 0.0000   |
| $\bar{K}_{L,r}$ | 0.0140   | 0.0128   | 0.0134   | 0.0000   | 0.0148   | 0.0000   | 0.0000   |
| $K_{L,\psi}$    | 0.4673   | 0.0000   | 0.5771   | 0.7275   | 0.0000   | 0.0000   | 0.6402   |
| $K_{L,\dot{r}}$ | -0.0001  | -0.0003  | 0.0000   | 0.0001   | 0.0000   | -0.0002  | 0.0000   |
| $\bar{K}_{N,p}$ | -0.0002  | 0.0002   | -0.0001  | 0.0000   | -0.0015  | 0.0000   | 0.0000   |
| $K_{N,\phi}$    | -0.3641  | 0.0000   | -0.4362  | -0.4119  | 0.0000   | 0.0000   | -0.3329  |
| $K_{N,\dot{p}}$ | 0.0001   | 0.0003   | 0.0000   | -0.0001  | 0.0000   | 0.0002   | 0.0000   |
| $\bar{K}_{N,r}$ | 0.0357   | 0.0365   | 0.0359   | 0.0000   | 0.0342   | 0.0000   | 0.0000   |
| $K_{N,\psi}$    | -0.0210  | 0.0000   | 0.0377   | 0.1619   | 0.0000   | 0.0000   | 0.4064   |
| $K_{N,\dot{r}}$ | -0.0001  | 0.0000   | 0.0000   | -0.0004  | 0.0000   | -0.0004  | 0.0000   |

**Table 4.12:** The 95% confidence intervals for the control gains of  $H_3(s)$ .

|                 |         |         |
|-----------------|---------|---------|
| $K_{L,p}$       | 0.0182  | 0.0308  |
| $K_{L,\phi}$    | 0.4389  | 0.9023  |
| $K_{L,\dot{p}}$ | 0.0000  | 0.0003  |
| $\bar{K}_{L,r}$ | 0.0072  | 0.0208  |
| $K_{L,\psi}$    | 0.2275  | 0.7072  |
| $K_{L,\dot{r}}$ | -0.0002 | 0.0000  |
| $\bar{K}_{N,p}$ | -0.0064 | 0.0061  |
| $K_{N,\phi}$    | -0.5339 | -0.1944 |
| $K_{N,\dot{p}}$ | -0.0000 | 0.0003  |
| $\bar{K}_{N,r}$ | 0.0291  | 0.0424  |
| $K_{N,\psi}$    | -0.2005 | 0.1585  |
| $K_{N,\dot{r}}$ | -0.0003 | 0.0000  |

$$H_3(s) = \begin{bmatrix} H_{L,p} & H_{L,r} \\ H_{N,p} & H_{N,r} \end{bmatrix} \quad (4.26)$$

$$H_{L,p}(s) = \left( 0.025 + 0.67 \frac{1}{s} + 0.0001s \right) e^{-s0.052} \quad (4.27)$$

$$H_{L,r}(s) = \left( 0.014 + 0.467 \frac{1}{s} - 0.0001s \right) e^{-s0.052} \quad (4.28)$$

$$H_{N,p}(s) = \left( 0 - 0.364 \frac{1}{s} + 0.0001s \right) e^{-s0.052} \quad (4.29)$$

$$H_{N,r}(s) = \left( 0.036 - 0.021 \frac{1}{s} - 0.0001s \right) e^{-s0.052} \quad (4.30)$$

Figure 4.15 shows that the global model explains the responses to  $r$  and  $p'$  qualitatively less well than it does for the responses to  $p$  and  $r'$ . The question is whether this qualitatively worse fit is due to a higher grade of variability, different time delays, or due to other factors that differ between the responses to  $r$  and  $p'$  and  $p$  and  $r'$ . The AICc values of  $H_1(s)$  and  $H_2(s)$  sum up to 331 whereas the AICc value of the global model  $H_3(s)$  is 342. Hence, the performance of the two separate PI-models is slightly better than that of the global model. The time delays of the individual models are 0.047 s and 0.060 s. Considering an average confidence interval of the time delay of  $\pm 5$  ms (section 3.6) these delays are different, but only within a small margin. Also, the global model includes a derivative component whose benefit for a biological sensory system is difficult to interpret. It does not make sense for an insect to heavily rely on derivative control because its erratic motion and unpredictable encounter of disturbances would lead to a large derivative feedback and a potentially unstable system. The asymmetry in the magnitude responses and the time delay are the main arguments for the global model  $H_3(s)$  to not perform

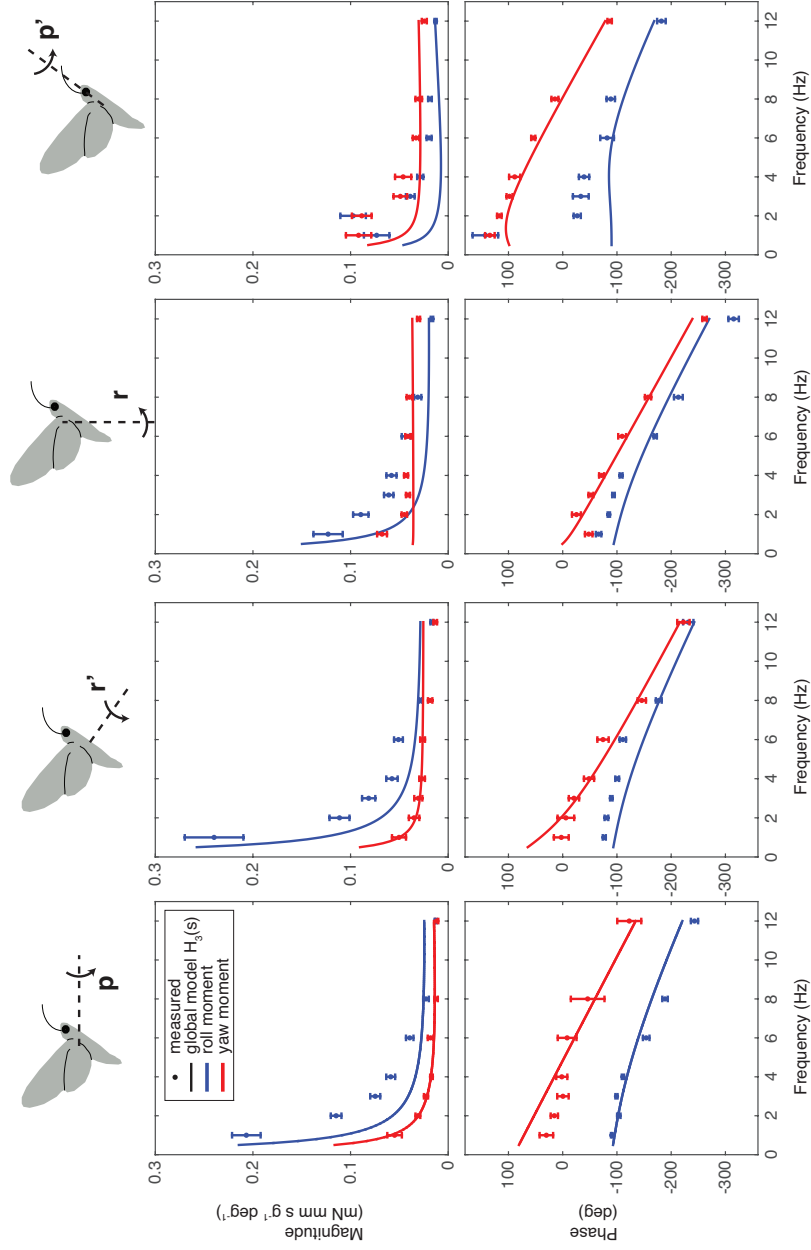


**Figure 4.15:** The control models that best explain the total response behaviour to the four types of lateral stimuli ( $p$ ,  $r$ ,  $p'$ , and  $r'$ ) are PID-controllers with a time delay of 0.052 s (full line). The colours indicate the roll (blue) and the yaw (red) response moment. Datapoints show the mean of individual means  $\pm$ SEM.

considerably better than the two individual models.

## 4.6 Discussion

The aim of this chapter was to explore how the behaviour changes as a function of the apparent body rotation axis. For this, I fitted vision-based flight control models and then evaluated to what extent these models could be generalised by testing spatial superposition. I fitted conventional PID-models to the optomotor responses to six different types of apparent body rotations:  $p$ ,  $q$ ,  $r$ ,  $p'$ ,  $r'$ , and  $p''$ . These models quantify the spatiotemporal parameters of the visual field that are relevant to flight control and stabilisation. The responses to longitudinal pitch stimuli were best explained by a PI-controller with a time delay of 0.042 s. The global control model for lateral stimuli is a PID-controller with a time delay of 0.052 s. But a better AICc value, i.e. a better model performance, is achieved by separating the responses to lateral stimuli into two groups. The first group consists of the responses to  $p$  and  $r'$  which are best explained by a PI-controller with a time delay of 0.047 s. The second group consists of the responses to  $r$  and  $p'$  which are best explained by a PI-controller with a time delay of 0.060 s. The linear superposition of the control laws that generate the responses to  $p$  and  $q$  reliably predicts the responses to combined lateral-longitudinal stimuli  $p''$  with frequencies below 6 Hz. Hence, spatial superposition holds for optic flow fields that indicate a combined lateral and longitudinal motion. But for lateral stimuli, the theory of spatial superposition only holds for a subset of controllers. As a consequence, we cannot linearly interpolate across PI-controllers to infer the control law for an arbitrary lateral stimulus.

The main caveat in this chapter is that by choosing the angular velocity as the stimulus, I potentially introduce an artificial effect of frequency in the magnitude responses. I tested

for such an effect by fitting PD-models to the response data resolved for the angular position as stimulus and found the gains and the time delays to be equivalent for the two different definitions of the stimulus. Hence, the control models are fitted to a real behavioural response rather than to an artificial effect of dividing by the frequency. Other caveats are that I fitted models to the lumped moment responses in the case of lateral stimuli. And I did not allow for separate time delays for the proportional and integral feedback (e.g. [7] [42]). But if I had allowed for these additional degrees of freedom, the models would have been overfitted.

The fact that PI-controllers best explain the relationship of the moment responses and the visual stimuli does not come as a surprise. Studies of the vision-based control in tethered [6] [5] and free flying [62] *Drosophila* also suggest a feedback of angular rate and position. Windsor et al. [9] looked at the control parameters required to stabilise the inherent instabilities described by the linearised flight dynamic models of *Hyles lineata*, whereas I derived the control parameters from empirical data. Nonetheless, they concluded that in order to stabilise an unstable manoeuvre that involves roll motion, a feedback of roll angle would suffice and that the additional feedback of roll rate would improve stability. In order to stabilise an unstable manoeuvre that involves pitch motion, they conclude that the feedback of either pitch rate or pitch angle would suffice, but that the combined feedback of pitch rate and angle improves stability. Cheng et al. [42] fitted a PI-controller to the free-flight responses of *M. sexta* to a sudden frontal visual stimulus. Their proportional and integral feedback gains of pitch rate and angle have been derived by comparing the free flight responses to the passive flight dynamics which had been measured on a dynamically scaled robotic wing. In their study, the proportional gain  $K_q$  is  $7.49 \times 10^{-6}$  N m s rad<sup>-1</sup>, and the integral gain  $K_\theta$  is  $1.13 \times 10^{-4}$  N m rad<sup>-1</sup>. Hence, their gains match surprisingly well to those fitted in  $H_{M,q}(s)$ , which are  $K_q = 5.31 \times 10^{-6}$

$\text{N m s rad}^{-1}$  and  $K_\theta = 1.48 \times 10^{-4} \text{ N m rad}^{-1}$ . The time delays of the fitted controllers match well with the initial estimates given in section 3.6, and also lie within the range reported by other studies of optomotor responses of *M. sexta*: Cheng et al. [42] suggest a time delay of  $\leq 0.063 \text{ s}$ ; Dyhr et al. [41] reported a visual-abdominal reflex of tethered *M. sexta* to pitch stimuli with a time delay of  $0.041 \text{ s}$ .

Spatial superposition across responses to lateral stimuli could be prevented at three different stages of the motion vision pathway. First, the individual control signals that are delivered by the subcomponents of the optic flow fields, i.e. by the wide-field direction-selective interneurons, may not be linearly integrated. Second, spatial superposition may be prevented because the time delay varies as a function of the rotational axis. For instance, Horridge et al. [61] found slow and fast processing direction-selective interneurons in diurnal species. Hence, I am unable to predict the control law to an arbitrary stimulus because the control laws with different time delays are not interchangeable. The different time delays could be caused by differences in the visual processing pathway, and could additionally also be affected by the extent to which other sensory modalities contribute to the response. Note that a control system with a large variation of time delays could represent a underdetermined system which is fundamentally unidentifiable. Third, spatial superposition is prevented at the level of the flight actuator. In this case, the measured responses are not predictable because the flight motor cannot operate with a linear increase or decay in moment responses due to physical limitations.

## 4.7 Conclusion and outlook

I conclude that the differences in vision-based flight control mechanisms could be a consequence of gaze stabilisation (discussed in the previous chapter), and due to the segregation

of the motion vision pathways for the different spatial composition of rotational flow fields. In the next chapter, I will explore whether the flight control models derived in this chapter stabilise the flight of a freely hovering moth. This will provide a basis to discuss how this difference in time delays may be of functional benefit in light of the moth's flight dynamics.

## Chapter 5

# The role of vision-based flight controllers in stabilising the flight dynamics

In the previous chapter, I identified the vision-based flight controllers based on an extensive set of measured optomotor responses. In this chapter, I combine these controllers with the moth's flight dynamics. The flight dynamics relate the forces and moments that the moth generates to the kinematics that these forces would produce in free flight. The most common way of describing the linearised flight dynamics is shown in equation 5.1, where  $\mathbf{A}$  is the system matrix,  $\mathbf{B}$  is the control matrix,  $\mathbf{x}(t)$  is the state vector, and  $\mathbf{u}(t)$  is the control input.

The components of  $\mathbf{A}$  describe how the aerodynamic forces  $X$ ,  $Y$ ,  $Z$  and aerodynamic moments  $L$ ,  $M$ ,  $N$  change as a function of the state variables  $\mathbf{x}(t) = [u, v, w, p, q, r, \phi, \theta, \psi]^T$  (all variables are described in figure 2.3). These nine state variables are the forward, sideways and vertical velocity; the roll, pitch and yaw rate; and the roll, pitch and yaw

angle, respectively. These state variables fully describe the moth's attitude and motion in space. The active control of the flight dynamics is described by the control matrix  $\mathbf{B}$  and the control signal  $\mathbf{u}(t)$ .

$$\dot{\mathbf{x}}(t) = \mathbf{A}\mathbf{x}(t) + \mathbf{B}\mathbf{u}(t) \quad (5.1)$$

Flight dynamic models form the basis of flight control studies and have therefore been widely studied for a number of species (bumblebee [65], fruit fly [66], locust [40], moth [36] [34] [67]). Flapping flight is non-linear and very complex due to its time-varying forces and moments, moving centre of mass, and changing inertia. Hence, the flight dynamics are often defined for a rigid body approximation of an insect. This allows three major simplifications: i) The rigid body motion is limited to six degrees of freedom, namely forward, sideways and vertical translation, and roll, pitch and yaw rotation. The forces and moments associated with these motion patterns are resolved at the centre of mass, whose location is constant for a non-deforming rigid body. ii) Most of these models assume that the wingbeat motion is much faster than any body dynamics of interest. Therefore, the effect of flapping wings on the insect's body is wingbeat-cycle-averaged. iii) In order to solve the equations of motion that describe the changes of the forces and moments generated by these rigid bodies, the models are linearised. This means that they only qualify to describe the changes of the flight dynamics for small disturbance quantities from an equilibrium state. This linearisation also leads to a decoupling of the longitudinal and lateral modes, which are explained in more detail later on.

Because the components of the system matrix  $\mathbf{A}$  are usually established from computational models and are provided in a non-dimensional form, I will first redimensionalise the system matrix  $\mathbf{A}$  with the morphological and inertial data of the moths used in these

experiments. This redimensionalisation is performed in section 5.1. In section 5.2, I apply the eigenvalue analysis on  $\mathbf{A}$  and hereby show what previous studies showed in the non-dimensional form, namely that the insect is inherently unstable. Hence, in the absence of a controller, the moth is not able to recover its equilibrium state after having experienced a small disturbance. In section 5.3, I combine  $\mathbf{A}$  with the active control described by  $\mathbf{Bu}(t)$ . This allows me to explore whether the empirically derived vision-based flight controllers are sufficient to stabilise the moth's inherent instabilities.

## 5.1 Redimensionalisation of the passive flight dynamics

As mentioned above, the components of the system matrix  $\mathbf{A}$  are usually established from computational models and are provided in a non-dimensional form. Computational models are used because the system matrix  $\mathbf{A}$  describes the body motion in response to an external disturbance and in absence of active control. It is very hard to derive these dynamics from a flying insect. In order to understand the flight dynamics of the hawkmoth, I redimensionalise the system matrix  $\mathbf{A}$  with the morphological and inertial data of the moths used in the experiments. The morphological and inertial data for *M. sexta* are given in tables 5.1 and 5.2.

The inertia tensor is a key parameter in the flight dynamics because it determines the angular acceleration that a moth experiences as a consequence of a moment acting on the body. A given moment will lead to a large angular acceleration if the inertia is small, and to a small angular acceleration if the inertia is large. The diagonal components of the inertia tensor  $I_x$ ,  $I_y$  and  $I_z$  are called moments of inertia and relate to the inertia about the body axes. The non-diagonal term of the inertia tensor  $I_{xz}$  is called a product of inertia and is non-zero by definition unless the x- and z-axes are principal axes (the

**Table 5.1:** Parameters used to redimensionalise the system matrix **A**. The body mass and length are the mean values for the 42 specimens used in the experiments. The wing parameters were measured on a sample moth. Parameters denoted with \* are from Liang et al. [67].

| Variable                               | Symbol   | Unit               | Measurement |
|----------------------------------------|----------|--------------------|-------------|
| <i>Body parameters:</i>                |          |                    |             |
| mass                                   | $m_b$    | mg                 | 1689        |
| length                                 | $l_b$    | mm                 | 47.1        |
| <i>Wing parameters:</i>                |          |                    |             |
| mass of one main wing                  | $m_{mw}$ | mg                 | 22.1        |
| mass of one hind wing                  | $m_{hw}$ | mg                 | 8.2         |
| length of one main wing                | $l_{mw}$ | mm                 | 48.94       |
| length of one hind wing                | $l_{hw}$ | mm                 | 30.42       |
| mean chord length*                     | $c$      | mm                 | 18.37       |
| radius of second moment of wing area*  | $r_2$    | mm                 | 24.74       |
| stroke amplitude*                      | $\phi$   | °                  | 114.4       |
| wingbeat frequency                     | n        | Hz                 | 24.1        |
| wingbeat period                        | T        | s                  | 0.038       |
| wing area for one set of wings (mw+hw) | $S_t$    | mm <sup>2</sup>    | 945.95      |
| fluid density                          | $\rho$   | kg m <sup>-3</sup> | 1.23        |

**Table 5.2:** The moth's inertia about the body's centre of mass. The inertial properties are defined for a body-fixed coordinate system with x aligned with the horizon and z aligned with gravity and a body pitch angle of  $\theta = 56.6^\circ$ . The total contribution of wing inertia (two main and two hind wings) to  $I_x$  and  $I_z$  is  $36.4 \times 10^{-9}$  kg m<sup>2</sup>.

| Variable                                | Symbol   | Unit                               | body  | winged body |
|-----------------------------------------|----------|------------------------------------|-------|-------------|
| roll moment of inertia                  | $I_x$    | kg m <sup>2</sup> $\times 10^{-9}$ | 157.7 | 194.1       |
| pitch moment of inertia                 | $I_y$    | kg m <sup>2</sup> $\times 10^{-9}$ | 214.9 | 214.9       |
| yaw moment of inertia                   | $I_z$    | kg m <sup>2</sup> $\times 10^{-9}$ | 83.5  | 120.0       |
| product of inertia between roll and yaw | $I_{xz}$ | kg m <sup>2</sup> $\times 10^{-9}$ | -86.1 | -86.1       |

remaining products of inertia,  $I_{xy}$  and  $I_{yz}$  are zero by symmetry). The practical effect of this non-zero product of inertia is that a moment around the x-axis will cross couple into a rotation around the z-axis and vice-versa. Inertia is measured in  $\text{kg m}^2$ . Effectively, the inertia reflects to what extent a moth will experience a resistance for moments about particular axes due to body mass that lies at a distance perpendicular to the rotation axis.

I estimated the inertia tensor by assuming that the density of the moth is uniform, and by assuming that the cross-section of the moth is circular in every transverse plane normal to the body long axis. The diameter of these circles are measured from a side-view of the moth (i.e. looking along the y-axis, figure 5.1, A). The 3D reconstruction of the body was generated in ImageJ software (version 1.45s, [68], National Institute of Health, Bethesda, MD) where I used the plugin BoneJ.jar and the body parameters from table 5.1 to calculate the inertia tensor  $\mathbf{I}$ , containing the moments of inertia about the body's principal axes  $I_x$  (the longitudinal body axis),  $I_y$ , and  $I_z$  (the inertia about the axis aligned with gravity) (figure 5.1, B). Using this method, the CoM was located at 0.44 body lengths from the head. This estimate is identical to two decimal places with the experimentally estimated location of the CoM in section 2.5. The inertia tensor in table 5.2 is given for a moth with a pitch angle of  $+56.6^\circ$ .

Although the wing mass is only about 4% of the body mass, the distance of the wing mass to the body x- and the z-axis is large. The wing inertia was calculated by treating equidistant wing sections (figure 5.1, D) as point masses along a thin rod connected to the centreline of the moth's body with an estimated diameter of 10mm [69]. Although the contribution of the wing to the total moment of inertia will vary cyclically through a wingbeat, I approximated this contribution by simply calculating the moment of inertia with the wing long axis parallel to the transverse y-axis of the body (i.e. with the wing

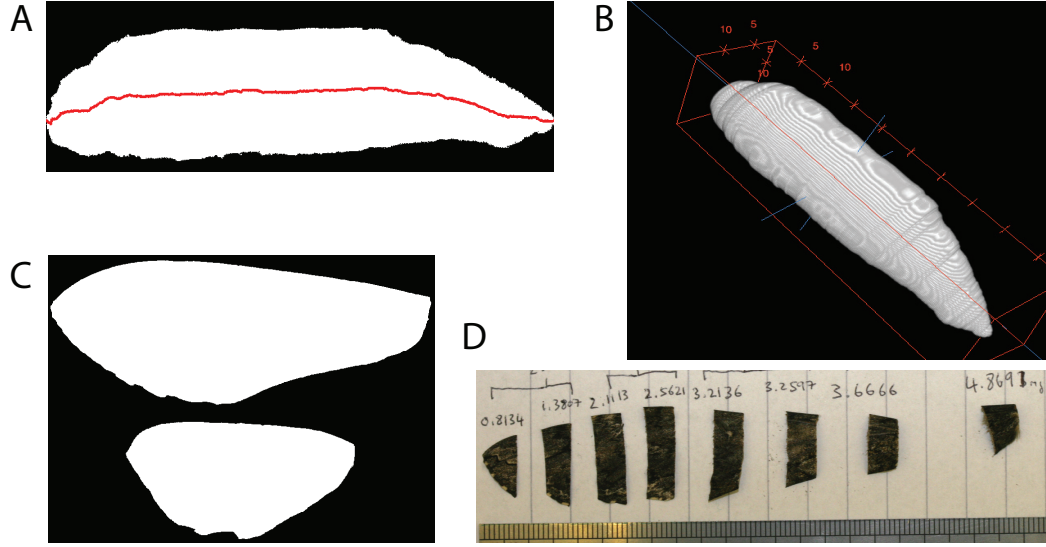


**Figure 5.1:** The inertia tensor of the body was evaluated using (A) a side-on view of the moth with the midpoints of each cross-section marked in red, and (B) a 3D reconstruction of the body with a constant density and without wings. The inertia of the wings was evaluated using (D) weighed sections of the wings. The outline of the main and hind wings (C) was used to calculate the wing surface area.

at close to its mid-stroke position).

The surface area of one pair of main and hind wing was evaluated by counting the pixels of the binary wing outlines (figure 5.1, C) in MATLAB and using the reference length of the wings in table 5.1.

As mentioned previously, the linearisation of the flight dynamic models by Zhang et al. [34] [35] leads to a decoupling of the longitudinal flight dynamics from the lateral flight dynamics. Hence, I have two separate system matrices  $\mathbf{A}_{\text{longitudinal}}$  and  $\mathbf{A}_{\text{lateral}}$  that describe the passive flight dynamics of the hawkmoth. The longitudinal flight dynamics describe changes in the forward force  $X$ , the vertical force  $Z$  and the pitch moment  $M$  as a function of small disturbances in the state vector  $\mathbf{x}_{\text{longitudinal}}(t) = [u, w, q, \theta]^T$ , i.e. small disturbances in forward velocity  $\delta u$ , in vertical velocity  $\delta w$ , in pitch rate  $\delta q$  and in pitch

angle  $\delta\theta$  about an equilibrium state (figure 5.2). The theory of longitudinal flight stability of *M. sexta* has been studied by Sun et al. [36], Zhang et al. [34], Liang et al. [67], and Cheng et al. [42]. I take the aerodynamic derivatives for the non-dimensional components of  $\mathbf{A}_{\text{longitudinal}}$  from Zhang et al. [34] where they are defined for a winged body at a free body angle of  $54.8^\circ$ . The redimensionalised system matrix is  $\mathbf{A}_{\text{longitudinal}}$ . A positive aerodynamic derivative such as  $M_u$  means that a positive disturbance  $\delta u$ , i.e. a forward velocity, will lead to a positive pitch moment  $M$ . A negative aerodynamic derivative such as  $M_q$  means that a positive disturbance  $\delta q$ , i.e. a pitch up rate, will lead to a negative pitch moment  $M$ . Because of the small disturbance model, the angular rates  $p$ ,  $q$ , and  $r$  are equivalent to the time derivatives of the Euler angles  $\phi$ ,  $\theta$ , and  $\psi$ .

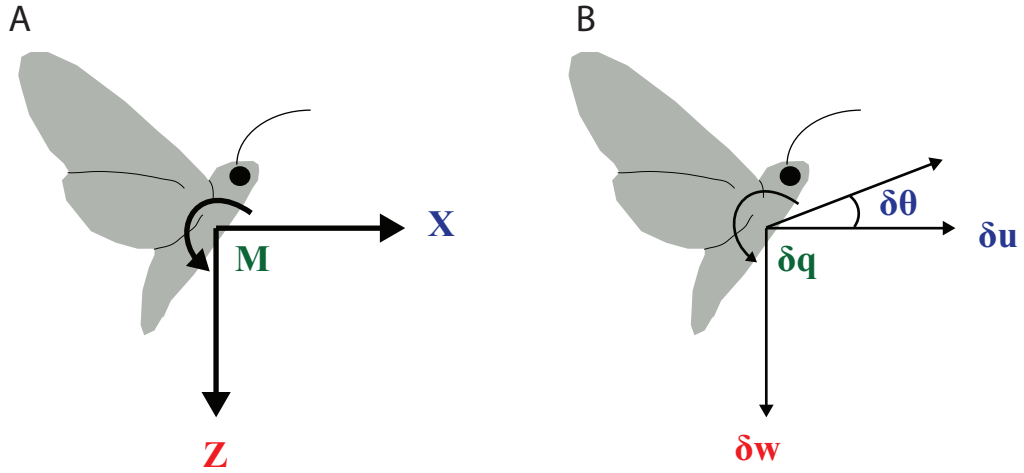


**Figure 5.2:** Longitudinal flight dynamics describe changes in the forward force  $X$ , the vertical force  $Z$  and the pitch moment  $M$  (shown in A) as a function of small disturbances in forward velocity  $\delta u$ , in vertical velocity  $\delta w$ , in pitch rate  $\delta q$  and in pitch angle  $\delta\theta$  (shown in B). At equilibrium,  $\delta u$ ,  $\delta w$ ,  $\delta q$  and  $\delta\theta$  are zero.

$$\mathbf{A}_{\text{longitudinal}} = \begin{bmatrix} \frac{X_u}{m} & \frac{X_w}{m} & \frac{X_q}{m} & -g \\ \frac{Z_u}{m} & \frac{Z_w}{m} & \frac{Z_q}{m} & 0 \\ \frac{M_u}{I_y} & \frac{M_w}{I_y} & \frac{M_q}{I_y} & 0 \\ 0 & 0 & 1 & 0 \end{bmatrix} = \begin{bmatrix} -3.20 & 0.26 & -0.03 & -9.81 \\ -0.25 & -1.82 & 0.01 & 0 \\ 624.87 & -0.26 & -6.03 & 0 \\ 0 & 0 & 1 & 0 \end{bmatrix}$$

The lateral flight dynamics on the other hand, describe changes in the side force  $Y$ , the roll moment  $L$  and the yaw moment  $N$  as a function of small disturbances of the state vector  $\mathbf{x}_{\text{lateral}}(t) = [v, p, r, \phi, \psi]^T$ , i.e. small disturbances in sideways velocity  $\delta v$ , in roll rate  $\delta p$ , in yaw rate  $\delta r$ , in roll angle  $\delta\phi$  (figure 5.3). Although the yaw angle  $\delta\psi$  has no aerodynamic effect, and hence no effect on the passive flight dynamics, we must nevertheless consider the dependence of the lateral forces and moments on the yaw angle  $\delta\psi$  to account for the dependence on yaw angle in the PI controller for yaw rate that was fitted in the previous chapter. The redimensionalised system matrix is  $\mathbf{A}_{\text{lateral}}$ . I take the aerodynamic derivatives for a winged body, i.e. the components of  $\mathbf{A}_{\text{lateral}}$  from Zhang et al. [35].

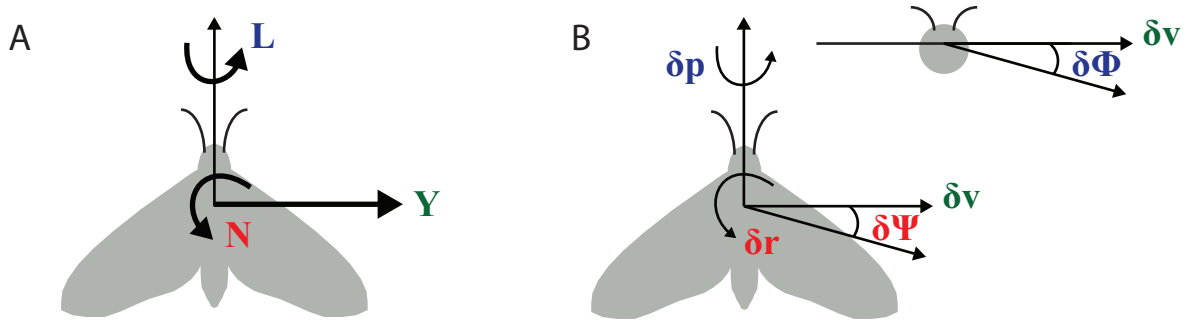


**Figure 5.3:** The lateral flight dynamics describe changes in the side force  $Y$ , the roll moment  $L$  and the yaw moment  $N$  (shown in A) as a function of small disturbances in sideways velocity  $\delta v$ , in roll rate  $\delta p$ , in yaw rate  $\delta r$ , in roll angle  $\delta\phi$  and in yaw angle  $\delta\psi$  (shown in B). At equilibrium,  $\delta v$ ,  $\delta p$ ,  $\delta r$ ,  $\delta\phi$  and  $\delta\psi$  are zero.

$$\mathbf{A}_{\text{lateral}} = \begin{bmatrix} \frac{Y_v}{m} & \frac{Y_p}{m} & \frac{Y_r}{m} & g & 0 \\ \frac{I_z L_v + I_{xz} N_v}{I_x I_z - I_{xz}^2} & \frac{I_z L_p + I_{xz} N_p}{I_x I_z - I_{xz}^2} & \frac{I_z L_r + I_{xz} N_r}{I_x I_z - I_{xz}^2} & 0 & 0 \\ \frac{I_{xz} L_v + I_x N_v}{I_x I_z - I_{xz}^2} & \frac{I_{xz} L_p + I_x N_p}{I_x I_z - I_{xz}^2} & \frac{I_{xz} L_r + I_x N_r}{I_x I_z - I_{xz}^2} & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \end{bmatrix} = \begin{bmatrix} -2.88 & -0.02 & 0.00 & 9.81 & 0 \\ 145.21 & -17.05 & 66.62 & 0 & 0 \\ -2.25 & 4.12 & -135.20 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \end{bmatrix}$$

## 5.2 Stability analysis of the passive flight dynamics

A system is stable if the effects of the small disturbances on the body decay with time, enabling the system to regain equilibrium. The solution  $\mathbf{x}(t)$  for  $\dot{\mathbf{x}}(t) = \mathbf{A}\mathbf{x}(t)$  is a function of the initial state of the system  $\mathbf{x}(t_0)$  and an exponential function of the system matrix  $\mathbf{A}$  and time  $t$  (equation 5.2).

$$\mathbf{x}(t) = \mathbf{x}(t_0)e^{\mathbf{A}t} \quad (5.2)$$

$$= \sum_{i=1}^{i=a} x_i(t_0) \mathbf{v}_i e^{\lambda_i t} \quad (5.3)$$

If the system matrix  $\mathbf{A}$  of order  $a$  can be diagonalised, it follows that the  $a$  eigenvalues  $\lambda_i$  and  $a$  eigenvectors  $\mathbf{v}_i$  of the system matrix  $\mathbf{A}$  are sufficient to fully describe the passive flight dynamics in the form of equation 5.3 [34] [9]. Hence, in order for the system to be stable, we want the disturbance motion to decay and that is achieved when the real parts of the complex eigenvalues are negative.

The theory underlying the eigenvalue analysis is widely applied in control theory and is very well documented. An eigenvalue can be a real number or a complex number, whereby complex values occur in conjugate pairs. A positive real eigenvalue indicates

an exponentially growing amplitude of motion where the body is moving away from its equilibrium position. This is called an unstable divergent mode. A negative real eigenvalue indicates an exponential decay in the amplitude of motion and the body will move back to its equilibrium position. This is called a stable subsidence mode. The imaginary part of a complex eigenvalue represents the angular frequency of an oscillatory motion. The mode is called an unstable or a stable oscillatory mode depending on whether the real part of the complex conjugate eigenvalue is positive or negative. If all eigenvalues of the system have a negative real component, the system is asymptotically stable. If one of the eigenvalues has a positive real component, the system will not get back to equilibrium and is therefore unstable. If one eigenvalue has a imaginary component with a zero real component, the system is marginally stable. In this case, the system will experience a sustained oscillation and not converge to equilibrium because the disturbance is neither amplified nor dampened. [65] The eigenvector indicates the magnitudes and the phases of the disturbance quantities relative to each other. The eigenvalue  $\lambda_i$  and its corresponding eigenvector  $\mathbf{v}_i$  represent a characteristic pattern of motion of the body which is called a natural mode of motion. As shown in equation 5.3, the passive response of the moth to an arbitrary disturbance from equilibrium is the linear sum of its exponentially growing or decaying natural modes of motion.

Solving for the eigenvalues and eigenvectors of  $\mathbf{A}_{\text{longitudinal}}$  gives us four longitudinal modes of motion, two of which form a complex conjugate pair. The results are given in tables 5.3 and 5.4. The time to half is the time required by a stable mode to halve its amplitude. The time to double is the time required by an unstable mode to double its amplitude.

The four modes of motion correspond to a fast, stable subsidence mode; a slow, stable subsidence mode; and a slow, unstable oscillatory mode. Sun et al. [36] analysed the

**Table 5.3:** The four eigenvalues of the redimensionalised longitudinal system matrix  $\mathbf{A}_{\text{longitudinal}}$  characterise the four longitudinal modes of motion of  $M. sexta$ .

|                                  | fast, stable subsidence | slow, stable subsidence | slow, unstable oscillation |
|----------------------------------|-------------------------|-------------------------|----------------------------|
| Eigenvalue                       | -21.13                  | -1.82                   | $5.95 \pm 15.95i$          |
| Time to half/ double (wingbeats) | 0.86                    | 9.94                    | 3.04                       |
| Time to half/ double (s)         | 0.03                    | 0.38                    | 0.12                       |
| Frequency (Hz)                   | -                       | -                       | 2.5                        |

**Table 5.4:** The eigenvectors of  $\mathbf{A}_{\text{longitudinal}}$  reflect the magnitude and phase of the disturbance variables  $\delta u$ ,  $\delta w$ ,  $\delta q$  and  $\delta \theta$  in each longitudinal mode of motion.

|                 | fast, stable subsidence |           | slow, stable subsidence |           | slow, unstable oscillation |           |
|-----------------|-------------------------|-----------|-------------------------|-----------|----------------------------|-----------|
|                 | magnitude               | phase (°) | magnitude               | phase (°) | magnitude                  | phase (°) |
| $\delta u$      | 0.51                    | 0         | 0.00                    | 0         | 0.54                       | 122       |
| $\delta w$      | 0.02                    | 0         | 38.21                   | 0         | 0.01                       | 327       |
| $\delta q$      | 21.13                   | 180       | 1.82                    | 180       | 17.03                      | 70        |
| $\delta \theta$ | 1                       | 0         | 1                       | 0         | 1                          | 0         |

mechanisms behind these modes of motion. Basically, the system matrix is simplified by ignoring the disturbance variables that play a minor role in the eigenvectors. The eigenvalues of the reduced model then explain the physical mechanisms for each mode. For instance, the fast, stable subsidence mode is driven by the coupled effect of  $\delta u$  and  $\delta q$  and the phase of the eigenvector shows that these two effects have a phase difference of  $180^\circ$ , i.e. are out of phase. Hence, a forward velocity  $\delta u$  causes a positive pitch moment ( $M_u > 0$ ). But the positive pitch rate  $\delta q$  then leads to a negative pitch moment ( $M_q < 0$ ). Hence, the moth will experience a forward velocity followed by a negative pitch moment or vice versa, a backward velocity followed by a positive pitch moment. This coupled effect counterbalances the disturbances and the moth converges back to the equilibrium state. The slow, stable subsidence mode is driven by the aerodynamic derivative  $Z_w$  which is negative in  $\mathbf{A}_{\text{longitudinal}}$ . Hence, if the body experiences a downwards velocity ( $\delta w > 0$ ) it will passively respond with a stabilising upwards force ( $Z < 0$ ). Else, if the

body experiences an upwards velocity ( $\delta w < 0$ ) it will passively respond with a stabilising downwards force ( $Z > 0$ ). Again, the damping effect of the body for a disturbance  $\delta w$  leads the moth back to equilibrium state. The slow, unstable oscillatory mode is driven by the aerodynamic derivative  $M_u$  which is positive in  $\mathbf{A}_{\text{longitudinal}}$ . But in contrast to the fast, stable subsidence mode, the eigenvalue for this mode shows that the coupling of  $\delta u$  and  $\delta q$  occur approximately in phase and therefore amplify the disturbance motion. Hence, the pitch-up moment which is caused by a forward velocity  $\delta u$  is enhanced by the positive disturbance  $\delta q$ . And the pitch-down moment that follows a backward velocity  $\delta u$  is enhanced by the negative disturbance  $\delta q$ . This leads to a motion that oscillates between a forward and upward motion and a backward and downward motion. This oscillation is unstable meaning that the moth moves away from its equilibrium state. In order to maintain stability, this particular mode of motion has to be recognised and actively controlled for by the moth. Animations of all longitudinal modes can be found in the supplementary information of the studies published by Windsor et al. [9].

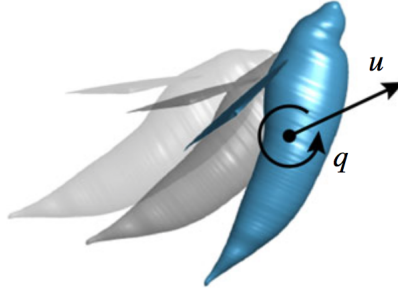


**Figure 5.4:** Diagram illustrating the slow, unstable oscillatory longitudinal mode. The mode couples the for-aft velocity  $u$  and the pitch rate  $q$ . Adapted from Windsor et al. [9].

The eigenvalue analysis of  $\mathbf{A}_{\text{lateral}}$  gives us four lateral modes of motion, two of which form a complex conjugate pair. For this study I added a fifth dimension to  $\mathbf{A}_{\text{lateral}}$  to account for the contribution of yaw angle in the feedback control. But the yaw angle does

**Table 5.5:** The four eigenvalues of the redimensionalised lateral system matrix  $\mathbf{A}_{\text{lateral}}$  characterise the four lateral modes of motion of *M. sexta*.

|                                  | slow, stable oscillation | fast, stable subsidence | slow, unstable divergence |
|----------------------------------|--------------------------|-------------------------|---------------------------|
| Eigenvalue                       | $-12.17 \pm 7.74i$       | -137.47                 | 6.68                      |
| Time to half/ double (wingbeats) | 1.25                     | 0.13                    | 2.71                      |
| Time to half/ double (s)         | 0.048                    | 0.005                   | 0.104                     |
| Frequency (Hz)                   | 1.23                     | -                       | -                         |

**Table 5.6:** The eigenvectors of  $\mathbf{A}_{\text{lateral}}$  reflect the magnitude and phase of the disturbance variables  $\delta v$ ,  $\delta p$ ,  $\delta r$  and  $\delta \phi$  in each lateral mode of motion.

|               | slow, stable oscillation |           | fast, stable subsidence |           | slow, unstable divergence |           |
|---------------|--------------------------|-----------|-------------------------|-----------|---------------------------|-----------|
|               | magnitude                | phase (°) | magnitude               | phase (°) | magnitude                 | phase (°) |
| $\delta v$    | 0.83                     | 219       | 0.10                    | 180       | 1.01                      | 0         |
| $\delta p$    | 14.42                    | 148       | 137.47                  | 180       | 6.68                      | 0         |
| $\delta r$    | 0.48                     | 142       | 248.72                  | 0         | 0.18                      | 0         |
| $\delta \phi$ | 1                        | 0         | 1                       | 0         | 1                         | 0         |

not play a role in the lateral flight dynamics and therefore does not add a fifth mode to the system. The results are given in tables 5.5 and 5.6 and match very well with the results found for *Hyles lineata* and animated in the supplementary information of the studies published by Windsor et al. [9]. The lateral flight modes consist of a slow, stable oscillatory mode; a fast, stable subsidence mode; and a slow, unstable divergence mode.

As mentioned previously, we can use a reduced model in order to clarify the physical interpretation of the modes, which has been done by Zhang et al. [33]. The slow, stable oscillatory mode is driven by the aerodynamic derivatives  $L_v > 0$  and  $L_p < 0$  [35] and looks similar to a dutch roll. The motion is triggered by a positive sideways velocity  $\delta v$  which leads to a negative roll moment  $L$ , i.e. a roll moment opposing the horizontal side velocity. The negative roll rate  $\delta p$  then leads to a counterbalancing positive roll moment. The two roll moments oppose each other and lead to an overall stable mode. The period of oscillation is 0.81 s and the time to half is 0.048 s. Hence, the disturbance motion is dampened before one cycle is completed, and it follows that although this is

strictly an oscillatory mode it will effectively have the character of a monotonic mode. The fast, stable subsidence mode is dominated by the aerodynamic derivatives  $L_p < 0$  and  $N_r < 0$  [33]. Hence, in response to a positive roll rate  $\delta p$  the body generates a negative roll moment. And in response to a positive yaw rate  $\delta r$  the body generates a negative yaw moment  $N$ . Hence, the body passively dampens the individual disturbance variables  $\delta p$  and  $\delta r$  by generating a moment in the direction opposing the roll rates and hereby leads the body back to an equilibrium state. The slow, unstable divergence mode is a coupled mode driven by the aerodynamic derivatives  $L_v > 0$  and  $L_p < 0$ . The positive side velocity  $\delta v$  leads to a roll moment in the same direction as the horizontal disturbance. Hence, this destabilises the body. Simultaneously, a positive roll rate  $\delta p$  leads to a damping roll moment. Although the magnitude for the disturbance  $\delta p$  is larger than that of  $\delta v$ , the dampening roll moment only slows down the mode and does not stabilise it. This leads to an overall slow, unstable divergence represented by a growing horizontal side velocity and a net roll moment pointing in the same direction (figure 5.5).

### 5.3 Stability analysis of the closed-loop system

The aim of this section is to evaluate whether the vision-based control models are sufficient to stabilise the flight dynamics in a closed-loop setup, i.e. to evaluate whether the empirical flight controllers stabilise the inherent instabilities. To address this question, I combine the redimensionalised system matrix  $\mathbf{A}$  of the passive flight dynamics with the control models derived in sections 4.3 and 4.5. As written out in equation 4.1 and shown in figure 4.5,  $\mathbf{u}(t)$  is the output of the controller and the input signal to the physical body, i.e. to the flight dynamics. I assume state feedback of the form

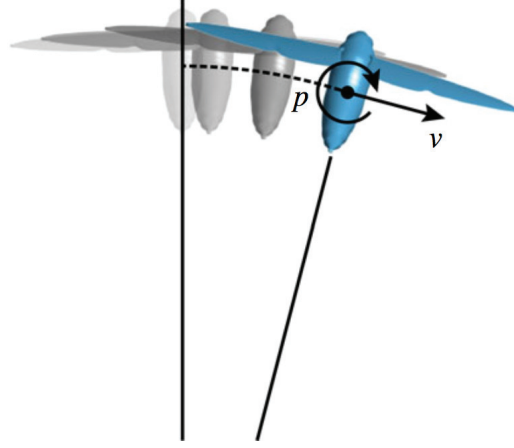


**Figure 5.5:** Diagram illustrating the slow, unstable lateral mode, adapted from Windsor et al. [9]. The sideways velocity  $\delta v$  leads to a roll moment in the same direction. This unstable motion is slowed down but not prevented by the negative roll moment produced in response to a positive roll rate  $\delta p$ .

$$\mathbf{u}(t) = -\mathbf{K}\mathbf{x}(t) \quad (5.4)$$

with  $\mathbf{K}$  as the gain matrix and  $\mathbf{x}(t)$  as the state vector. State feedback means that the control input to the flight dynamics is proportional to the state variables  $\mathbf{x}(t)$  rather than being an external force or moment. Substituting equation 5.4 into equation 5.5 leads to equation 5.6, and with  $-\mathbf{BK} = \mathbf{A}_c$  I then get the closed-loop system matrix  $(\mathbf{A} + \mathbf{A}_c)$  in equation 5.7.

$$\dot{\mathbf{x}}(t) = \mathbf{A}\mathbf{x}(t) + \mathbf{B}\mathbf{u}(t) \quad (5.5)$$

$$= (\mathbf{A} - \mathbf{BK})\mathbf{x}(t) \quad (5.6)$$

$$= (\mathbf{A} + \mathbf{A}_c)\mathbf{x}(t) \quad (5.7)$$

Hence, in order to analyse the stability of the closed-loop system I analyse the eigenvalues and eigenvectors of the closed-loop system matrices  $(\mathbf{A}_{\text{longitudinal}} + \mathbf{A}_{\text{c,longitudinal}})$  and  $(\mathbf{A}_{\text{lateral}} + \mathbf{A}_{\text{c,lateral}})$ . Because the eigenvalue decomposition is only applicable to a linear system, I need to transform the controller's exponential term for the time delay into a rational function. Among the many methods, Padé approximations (equation 5.8) are the most frequently used to approximate a dead-time or time delay in control system theory.

$$e^{-s\tau} \approx \frac{1 - k_1 s + k_2 s^2 + \dots \pm k_N s^N}{1 + k_1 s + k_2 s^2 + \dots + k_N s^N} \quad (5.8)$$

I used the *pade* function in MATLAB which replaces the time-delay  $e^{-s\tau}$  with the Nth-order Padé approximation. As shown in figure 5.6, for frequencies up to 12 Hz, the third order Padé approximation of  $e^{-s0.042}$  and  $e^{-s0.060}$  is good. A higher order approximation would provide a better fit at higher frequencies. Although, these higher order approximations are also more likely to introduce artefacts. Hence, for the subsequent stability analysis suffice it to use the third order approximation. As I will discuss later, this approximation affects the dynamics of the system by adding as many states and herewith eigenvalues to the model as orders in the approximation.

### 5.3.1 Closed-loop stability of the longitudinal flight dynamics

The control of longitudinal motion is performed by the PI-controller  $H_{M,q}(s)$  fitted in section 4.3: the pitch moment response  $M$  is proportional to pitch rate  $q$  and to pitch angle  $\theta$ . Hence, I get the following control system matrix  $\mathbf{A}_{\text{c,longitudinal}}$ :

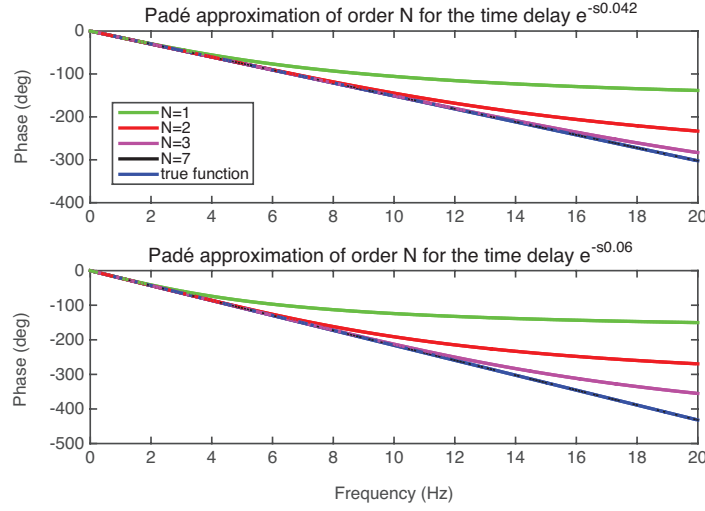


**Figure 5.6:** Padé approximation of order  $N$  for two different time delay functions  $e^{-s0.042}$  (top graph), and  $e^{-s0.06}$  (bottom graph). The real function (in blue) is approximated with a rational function of order  $N=1$  (green), 2 (red), 3 (magenta) and 7 (black). For frequencies up to 12 Hz, the third order approximation matches the true function sufficiently well.

$$\mathbf{A}_{c, \text{longitudinal}} = \begin{bmatrix} 0 \\ 0 \\ 1/I_y \\ 0 \end{bmatrix} \begin{bmatrix} 0 & 0 & -K_q & -K_\theta \end{bmatrix} = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & \frac{-K_q}{I_y} & \frac{-K_\theta}{I_y} \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

We know from previous section that the flight dynamics are unstable if the real part of the eigenvalue  $\lambda_i$  is positive. But in this section I am not only interested in the quantitative analysis but also want to expand on the qualitative effects of the time delay and the two feedback gains on the system's performance. I therefore discuss the stability of the closed-loop flight dynamics using root locus plots (e.g. figure 5.7). This graphical representation of the eigenvalues in the complex plane with the imaginary and real axis shows how the eigenvalues of the closed-loop system change as a control variable is varied.

An eigenvalue with a negative real component is located in the left plane, i.e. to the left of the axis with  $\text{Re}=0$ , and the system is stable. But an eigenvalue with a positive real component is located in the right plane where  $\text{Re}>0$ , and the system is unstable. Hence, the ranges of stability, instability, and the conditions that lead to an unstable system are clearly visualised in the root locus plots. In the left graph of figure 5.7 I compare the four eigenvalues of the passive flight dynamics (table 5.3) to those of the closed-loop system matrix ( $\mathbf{A}_{\text{longitudinal}} + \mathbf{A}_{\text{c,longitudinal}}$ ) for a time delay  $\tau=0$  s. In the absence of a time delay, the PI-controller shifts the two eigenvalues of the unstable oscillation from the right plane ( $\text{Re}>0$ ) into the left plane ( $\text{Re}<0$ ) and hereby renders the closed-loop system asymptotically stable. Simultaneously, the controller increases the frequency of the oscillatory mode from 2.5 Hz to 3.3 Hz. The imaginary axis indicates  $i\omega$  where  $\omega$  is the frequency  $2\pi f_m$ . And therefore, the modal frequency  $f_m$  is calculated as the imaginary component divided by  $2\pi$ . The eigenvalue of the slow, stable subsidence mode is not affected by the closed-loop feedback and remains at  $\lambda=-1.82$ . This is because the mode is driven by disturbances in vertical velocity  $\delta w$  rather than by the feedback variables pitch angle or pitch rate (table 5.4). The fast, stable subsidence mode on the other hand is driven by disturbances in pitch rate  $\delta q$ . The controller shifts the eigenvalue of that mode along the imaginary axis closer to  $\text{Re}=0$ .

On the other hand, when I include a time delay, the controller does not stabilise the closed-loop system any more (right graph in figure 5.7). On the contrary, the system becomes more unstable. The controller shifts the eigenvalues of the unstable oscillatory mode to more positive real values and also increases its modal frequency to 4.8 Hz. The eigenvalue of the slow, stable subsidence remains unaffected by the time delay. The eigenvalue of the fast, stable subsidence shifts further to the right, but still remains in the left plane. The third order Padé approximation also introduces three new eigenvalues

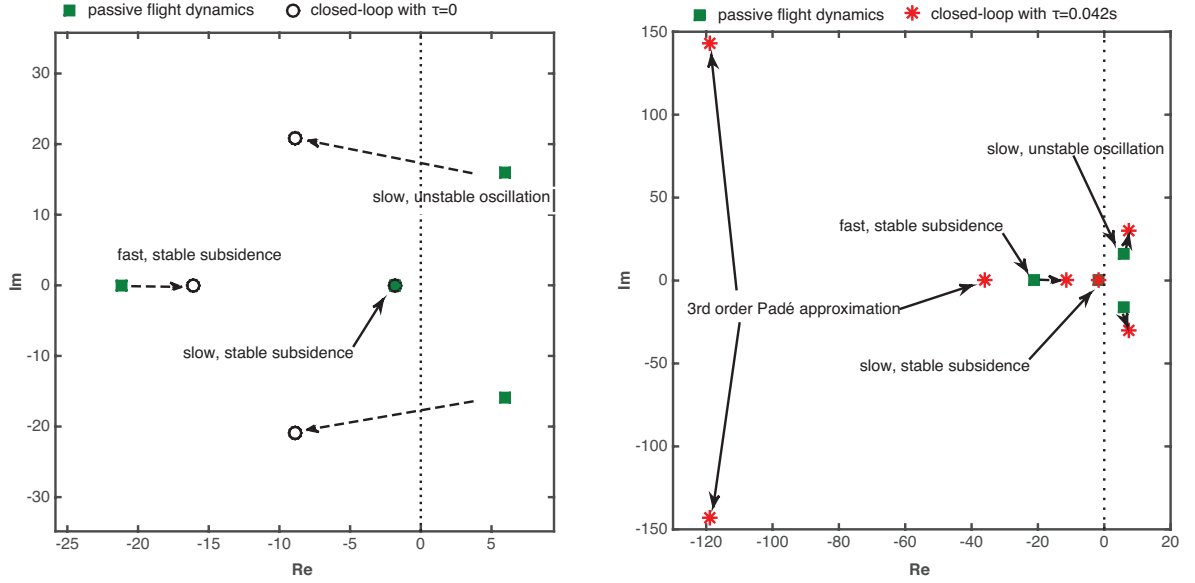


**Figure 5.7:** Root locus graphs showing the eigenvalues of the longitudinal flight dynamics. The left graph shows that the four eigenvalues of the passive flight dynamics (green squares) are stabilised by the fitted PI-controller  $H_{M,q}(s)$  with  $K_q = 5.31 \times 10^{-6} \text{ N m s rad}^{-1}$ ,  $K_\theta = 1.48 \times 10^{-4} \text{ N m rad}^{-1}$  and  $\tau=0$  (black circles), because all real parts of the four eigenvalues are in the left plane. The right graph shows that the eigenvalues of the unstable mode remain in the right plane for a closed-loop system with the same PI-controller, but with a time delay  $\tau=0.042 \text{ s}$  (red stars). Hence, the system remains unstable.

located at  $\lambda=-35.9$  and  $\lambda = -118.8 \pm 143i$ . In short, the fitted PI-controller does not stabilise the longitudinal flight dynamics. This means that the closed-loop model is either wrong (e.g. the linearised flight dynamic models are not applicable, or the model fitting method for the vision-based flight controllers is erroneous), or, the closed-loop model is incomplete (i.e. it needs to include other sensory feedback). On one hand, the system matrix  $\mathbf{A}_{\text{longitudinal}}$  is calculated for small disturbances from an equilibrium state where  $X = 0 \text{ N}$ ,  $Z = -mg \text{ N}$  and  $M = 0 \text{ N m}$ . But as already observed by Windsor et al. [9], the tethered moths generated on average a small excess forward thrust, did not provide full weight support, and generated a nose-down pitch moment, indicating that

they were not at an equilibrium state. This means that the vision-based controller represented in  $\mathbf{A}_{c, \text{longitudinal}}$  is not designed within the same limitations that the system matrix  $\mathbf{A}_{\text{longitudinal}}$  had been designed for. Additionally, the inertia terms would be larger if I had included the effect of added mass. This could increase the passive damping and put the system in a more stable position. On the other hand, the time delay is the most difficult parameter to identify in this system identification. The time delay of 0.042 s is the delay that minimises the mean squared error when looping across  $\tau=0$  to  $\tau=0.2$  s but following observations might give reason to assume that the fitted delay is too large to provide stability. Willmott et al. [57] mention that tethered specimens tend to demonstrate lower wingbeat frequencies than free flying specimens, and Heisenberg et al. [58] observed a larger phase lag for tethered species. Both a lower wingbeat frequency and larger phase lag could lead to a larger time delay of the optomotor system. Also, Sponberg et al. [28] explain that lower luminance levels require species to integrate over a larger time span and hereby increase their time delay.

In the remainder of this section I perform a sensitivity analysis in order to better understand the effect of the control variables on the closed-loop dynamics of longitudinal modes. Figure 5.8 illustrates the sensitivity of the closed-loop flight dynamics to a varying time delay of  $\tau = 0$  s to  $\tau = 0.050$  s, in intervals of 0.5 ms. For this I fixed the gains  $K_q$  and  $K_\theta$  according to the model  $H_{M,q}(s)$  in equation 4.12. The increasing time delay causes all eigenvalues, except that of the slow subsidence, to shift right, i.e. to become less stable. The eigenvalues of the oscillatory mode transition into the right plane for a delay  $\tau_{crit} \geq 0.027$  s. The destabilising effect of the time delay is likely to be caused by the increasing phase lag.

Next, as illustrated in the left graph of figure 5.9, I fix the time delay ( $\tau = 0.042$  s) and the integral feedback ( $K_\theta = 1.48 \times 10^{-4}$  N m rad<sup>-1</sup>), but I vary the proportional gain  $K_q$

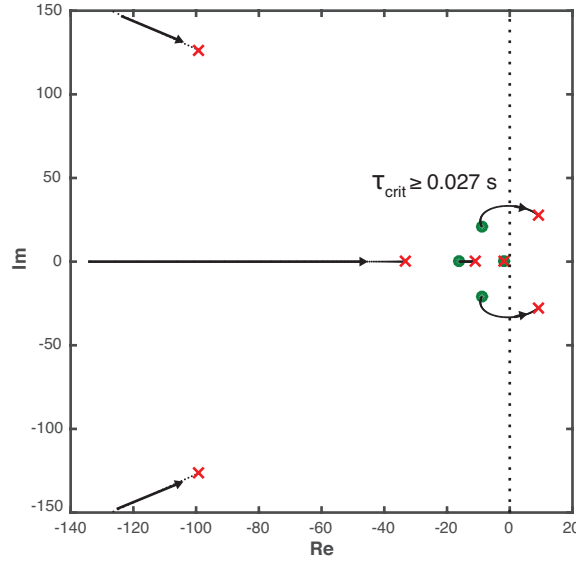


**Figure 5.8:** Root locus plot of the closed-loop system with the fitted gains  $K_q = 5.31 \times 10^{-6}$  N m s rad $^{-1}$ ,  $K_\theta = 1.48 \times 10^{-4}$  N m rad $^{-1}$ , and a time delay  $\tau$  that varies from 0 (green dots) to 0.050 s (red crosses). The four eigenvalues of the longitudinal flight dynamics are represented by the four green dots closest to the axis Re=0. For the given control parameters  $K_q$  and  $K_\theta$ , the two eigenvalues of the oscillatory mode become unstable at a delay of  $\tau_{crit} \geq 0.027$  s. The three eigenvalues of the third order Padé approximation (red crosses) remain on the far left.

from 0 to  $7.19 \times 10^{-6}$  N m s rad $^{-1}$ .

All other parameters kept constant, an increase in  $K_q$  makes the eigenvalues move to the left, rendering the system more stable. Nonetheless, even the highest tested value of  $K_q$  does not stabilise the system. But as illustrated in the right graphs of figure 5.9, if  $K_\theta = 0$  N m rad $^{-1}$ , then an increase in proportional gain  $K_q$  stabilises the system. This holds for a time delay of  $\tau = 0$  s and  $\tau = 0.025$  s. However, stability remains weak as the eigenvalues remain close to the axis of Re=0. Also, we see that for this pure proportional feedback of pitch rate, the eigenvalue of the fast, stable subsidence merges with an eigenvalue of the Padé approximation and eventually leads to a second unstable oscillatory mode (bottom right graph in figure 5.9).

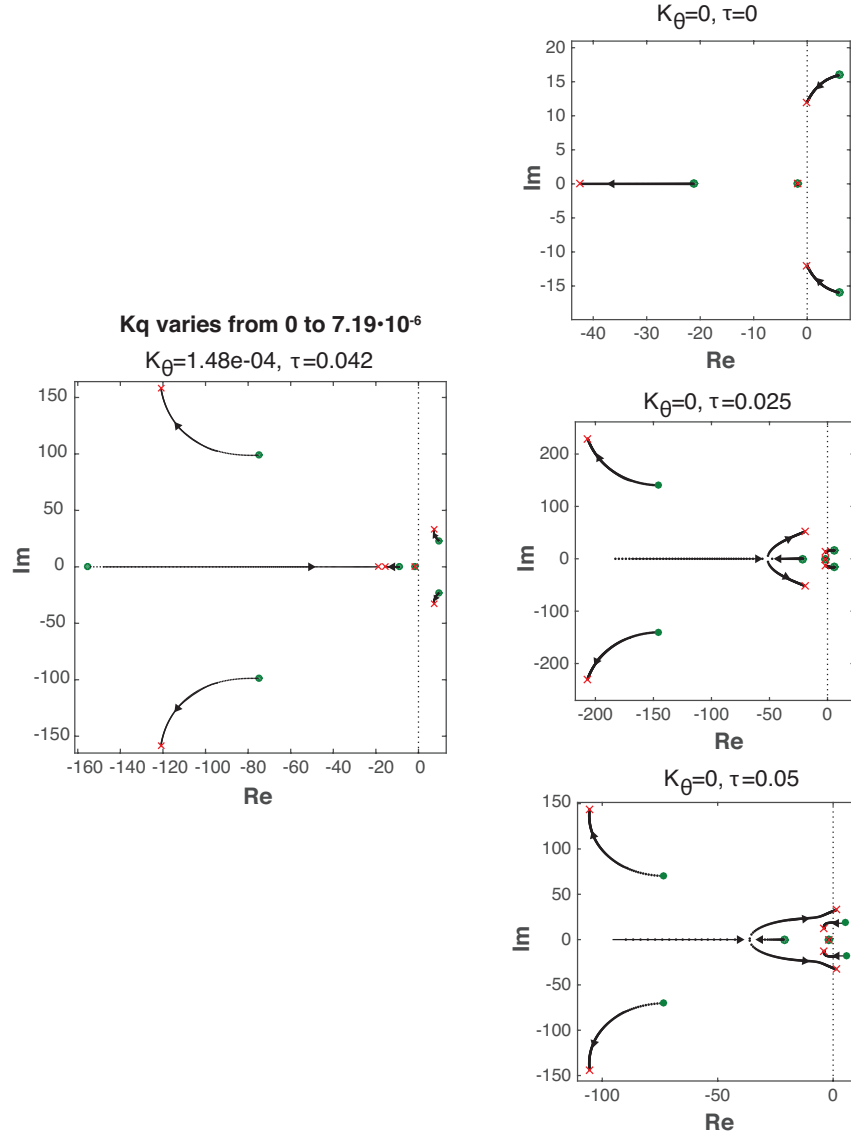


**Figure 5.9:** Root locus plots showing the effect of the gain on pitch rate which varies from  $K_q=0$  (green dot) to  $7.19 \times 10^{-6}$  N m s rad $^{-1}$  (red cross). The left graph shows the effect using the fitted control parameters  $\tau = 0.042$  s, and  $K_\theta = 1.48 \times 10^{-4}$  N m rad $^{-1}$ . The graphs to the right illustrate the effects of a pure proportional feedback ( $K_\theta = 0$  N m rad $^{-1}$ ) for  $\tau = 0$  s, 0.025 s, and 0.05 s, respectively.

Lastly, as illustrated in the left graph of figure 5.10, I fix  $\tau = 0.042$  s and  $K_q = 5.31 \times 10^{-6}$  N m s rad $^{-1}$ , but vary the integral feedback  $K_\theta$  from 0 to  $1.92 \times 10^{-4}$  N m

$\text{rad}^{-1}$ .

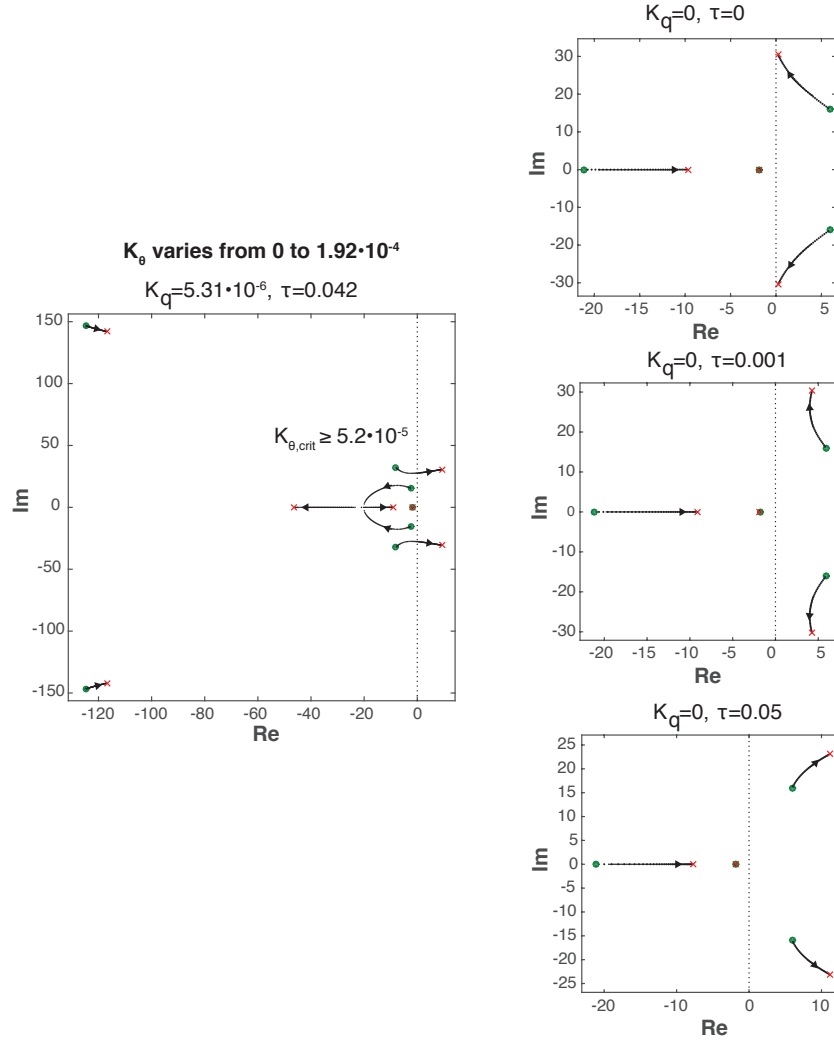


**Figure 5.10:** Root locus plots showing the effect of the gain on pitch angle which varies from  $K_\theta=0$  (green dot) to  $7.19 \times 10^{-6} \text{ N m rad}^{-1}$  (red cross). The left graph shows the effect using the fitted control parameters  $K_q=5.31 \times 10^{-6} \text{ N m s rad}^{-1}$  and  $\tau=0.042 \text{ s}$ . The graphs to the right illustrate the effects of a pure integral feedback ( $K_q=0 \text{ N m s rad}^{-1}$ ) for  $\tau = 0 \text{ s}$ ,  $0.01 \text{ s}$ , and  $0.05 \text{ s}$ , respectively.

When  $K_\theta = 0$ , the closed-loop flight dynamics are stable with all eigenvalues in the left plane. But an increasing gain on angular position causes the eigenvalues of the unstable oscillatory mode to transition to the right plane at  $K_{\theta, \text{crit}} = 5.2 \times 10^{-5} \text{ N m rad}^{-1}$ .

An increase in  $K_\theta$  also causes the second oscillatory mode with eigenvalues starting at  $\lambda = -2.27 \pm 15.36i$  to separate into two monotonic modes, one of which belongs to the Padé approximation and the other belongs to the fast subsidence mode. As we see in the right graphs of figure 5.10, where  $K_q = 0$ , the integral gain causes the oscillatory mode to move to higher frequencies. And more importantly, even if the time delay for the feedback of pitch angle is very small (e.g.  $\tau = 0.001$  s), the integral gain causes the unstable oscillatory mode to become even more unstable. It appears that the system can tolerate a higher delay in the proportional feedback than it can for the integral feedback. In the first instance it appears odd that the integral feedback promotes instability, even for a small time delay. What is the benefit of an integral gain in the flight control loop? It could for instance improve the flight qualities by preventing the bifurcation into the second oscillatory mode. Or it could change a modal frequency to prevent it from interfering with the wingbeat frequency.

I conclude that if there is no time delay, the fitted PI-controller stabilises the system. Also, if there is no time delay, each gain separately stabilises the system. If there is a non-zero time delay,  $K_q$  stabilises the system but also introduces a second oscillatory mode that eventually grows unstable. And even for a small time delay,  $K_\theta$  destabilises the system, but it also transforms the second oscillatory mode into two monotonic modes. This suggests that the instability of the closed-loop system with a time delay is caused by the instability of the integral gain which is driven by time delays.

In figure 5.11 we see how the three control variables interact. Each graph corresponds to a root locus plot with the four eigenvalues of the closed-loop system. In each graph, the time delay is varied for a fixed set of proportional and integral gain. The middle graph illustrates the closed-loop system for the fitted gains of  $H_{M,q}(s)$ , and we see that the PI-controller would only stabilise if  $\tau \leq 0.027$  s. If we move along the row we see the

effect of  $K_\theta$  and if we move along the column, we see the effect of  $K_q$ . For a time delay of zero, the system is always stable. The eigenvalue of the slow, stable subsidence remains independent of the three control variables. In the graphs b), c) and f) we see the merging of two monotonic modes into a second oscillatory mode. An increase in  $K_q$  stabilises the inherently unstable oscillatory mode but introduces this second oscillatory mode that grows unstable for  $\tau \geq 0.0295$  s. An increase in  $K_\theta$  shifts the eigenvalues of the unstable oscillation to the left and increases its modal frequency.

This sensitivity analysis in figure 5.11 delivers the same  $\tau_{crit}$ , independent of whether the Padé approximation is of third and for a seventh order. But the third order approximation is more conservative than the first order approximation. This is because  $\tau_{crit}$ , the time delay for which the system becomes unstable, is generally smaller for the third order approximation. Further studies are necessary to evaluate whether the bifurcation observed in the sensitivity analysis has a true physical meaning or whether it is an artefact of the Padé approximation.

An alternative explanation for why stability is not provided with pure visual feedback is that the model does not account for mechanosensory feedback. Due to the longer time delay that crepuscular species require for visual processing, multiple studies have investigated the function of antennae or wings in providing short latency angular rate feedback in Lepidoptera [70] [71]. Sane et al. [72] [73] concluded from antennectomy experiments that antennae are necessary for flight stability and control in *M. sexta* and suggests that rotational motion may be encoded with time delays  $< 0.01$  s. Hinterwirth et al. [46] show that antennal mechanosensory feedback during pitch stimuli mediate abdominal flexion in *M. sexta*. Elzinga et al. [74] report that fast mechanosensory feedback provides active damping which supplements the passive damping for the slow visual feedback. Hence, I imitate the effect of mechanosensory feedback of pitch rate by increasing the magnitude of the

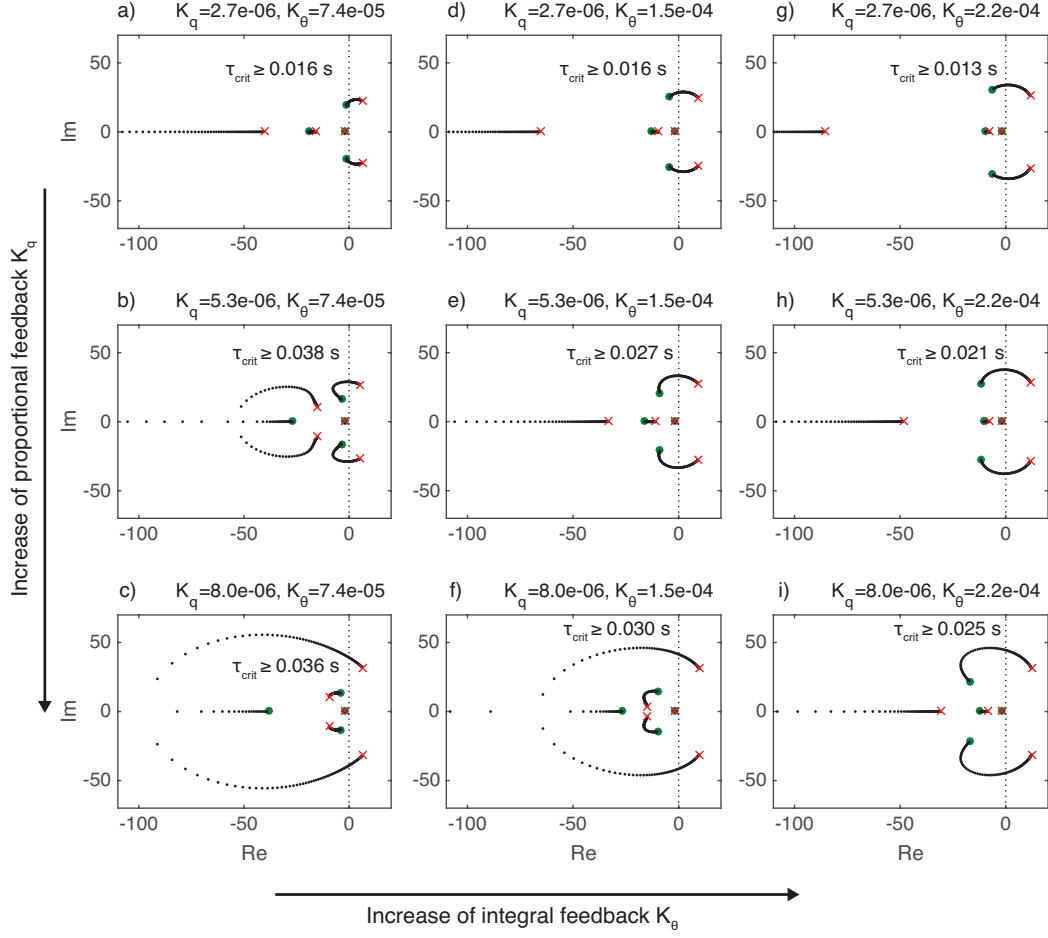


**Figure 5.11:** Root locus plots of the closed-loop longitudinal flight dynamics as a function of  $\tau$ ,  $K_q$  and  $K_\theta$ . The ordinate indicates the imaginary part of the eigenvalues and the abscissa indicates the real part of the eigenvalues. In each graph, the time delay  $\tau$  varies from 0 (green dot) to 0.05 s (red cross). The time delay is approximated by a third order Padé approximation that introduces three eigenvalues, only one of which is visible on the far left in each graph. The middle graph illustrates the closed-loop system with the gains from the fitted PI-controller  $H_{M,q}(s)$ .

aerodynamic stability derivative  $M_q$  by 3.5 times, leading to a new value of  $\frac{M_q}{I_y} = -21.1 \text{ s}^{-1} \text{ rad}^{-1}$ . When this factor increases, the passive flight dynamics become stable and the PI-controller renders the system even more stable. With  $\frac{M_q}{I_y} = -21.1 \text{ s}^{-1} \text{ rad}^{-1}$ , the

modified system matrix  $\mathbf{A}_{\text{longitudinal}}$  still contains an unstable pair of eigenvalues for the oscillatory mode (left graph in figure 5.12). But if I now combine it with the empirically fitted vision-based flight controller, the unstable eigenvalues are now shifted into the left plane, making the system stable. Hence, by accounting for a prior pitch rate damping initiated by the mechanosensory feedback, the fitted vision-based flight controller  $H_{M,q}(s)$  can stabilise the system.

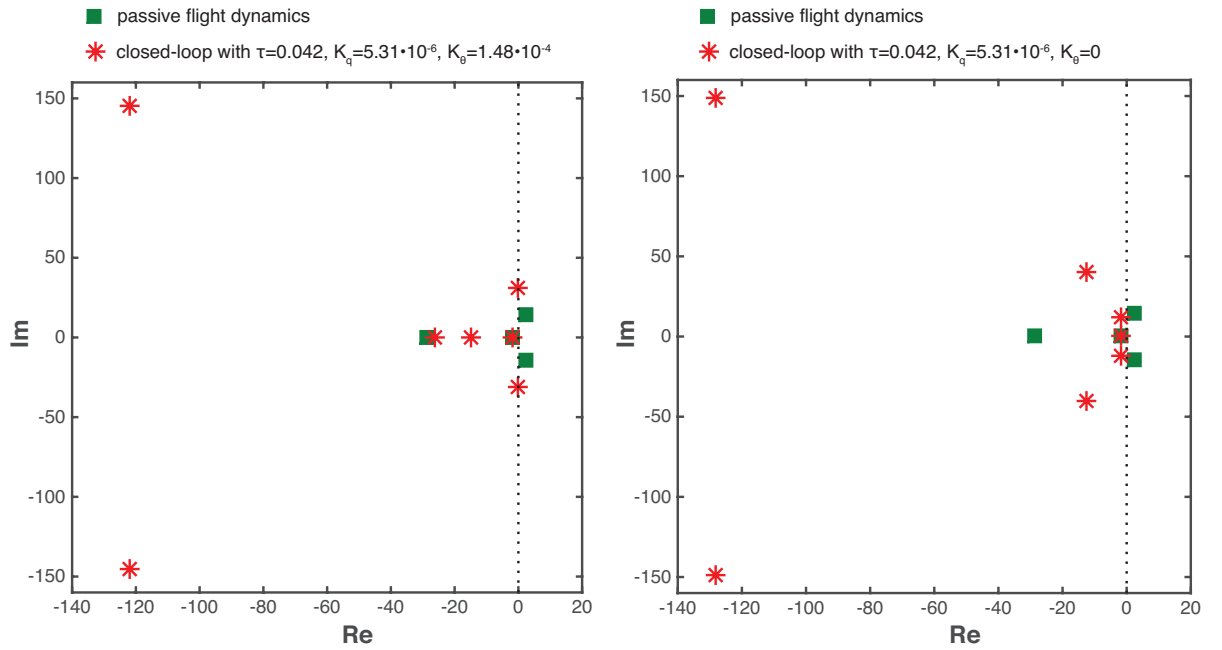


**Figure 5.12:** Root locus plot for a modified aerodynamic derivative  $M_q$  which accounts for added pitch rate damping due to mechanosensory feedback. The left graph shows that the combination of a modified  $\mathbf{A}_{\text{longitudinal}}$  with the fitted PI-controller stabilises the system. The right graph shows that this modified system is even more stable in the absence of an integral feedback.

In absence of the integral feedback ( $K_\theta = 0$ ), this modified system becomes more stable (right graph of figure 5.12), although it does introduce a bifurcation.

I conclude from this analysis of the longitudinal closed-loop hover flight dynamics that the PI-model  $H_{M,q}(s)$  is not sufficient to stabilise longitudinal motion. In order for the

model to stabilise the inherent instabilities, the controller is either not allowed to operate with a time delay, or, it needs to operate on a system which has experienced prior pitch rate damping. Based on the sensitivity analysis, I infer that the time delay affects the integral feedback such that it drives the system to become more unstable. Hence, this study is consistent with the hypothesis that longitudinal flight control and stability does not entirely rely on visual feedback and requires other sensory modalities to assess self-motion.

### 5.3.2 Closed-loop stability of the lateral flight dynamics

The two control inputs for the lateral flight dynamics are the roll moment  $L$  and the yaw moment  $N$ . Each control moment contains feedback of roll rate  $p$  and yaw rate  $r$  as well as feedback of roll angle  $\phi$  and yaw angle  $\psi$  (equations 4.16 - 4.19 and equations 4.21 - 4.24). Hence, each control moment has five control parameters with the time delay  $\tau$ . It follows that the system control matrix  $\mathbf{B}$  is a  $5 \times 2$  matrix with components in the second and third row. The gain matrix  $\mathbf{K}$  is a  $2 \times 5$  matrix with the first column containing zeros as I am not considering the feedback of the sideways velocity  $v$  in this control loop. The remaining four columns of  $\mathbf{K}$  contain the proportional and integral gains. This makes  $\mathbf{A}_{c,lateral}$  a  $5 \times 5$  matrix.

$$\mathbf{A}_{c,lateral} = -\frac{1}{I_x I_z - I_{xz}^2} \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & K_{L,p}I_z + K_{N,p}I_{xz} & K_{L,r}I_z + K_{N,r}I_{xz} & K_{L,\phi}I_z + K_{N,\phi}I_{xz} & K_{L,\psi}I_z + K_{N,\psi}I_{xz} \\ 0 & K_{L,p}I_{xz} + K_{N,p}I_x & K_{L,r}I_{xz} + K_{N,r}I_x & K_{L,\phi}I_{xz} + K_{N,\phi}I_x & K_{L,\psi}I_{xz} + K_{N,\psi}I_x \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

First, I analyse the performance of the PI-controllers for this multi-input, multi-output system  $H_1(s)$ . These control parameters had been derived from the responses to stimuli  $p$  (rotation about the horizontal x-axis) and  $r'$  (rotation about the dorso-ventral  $z'$ -axis). In the left root locus plot of figure 5.13 we see that the five eigenvalues of the passive lateral flight dynamics are stabilised by these PI-controllers if the time delay is set to zero.

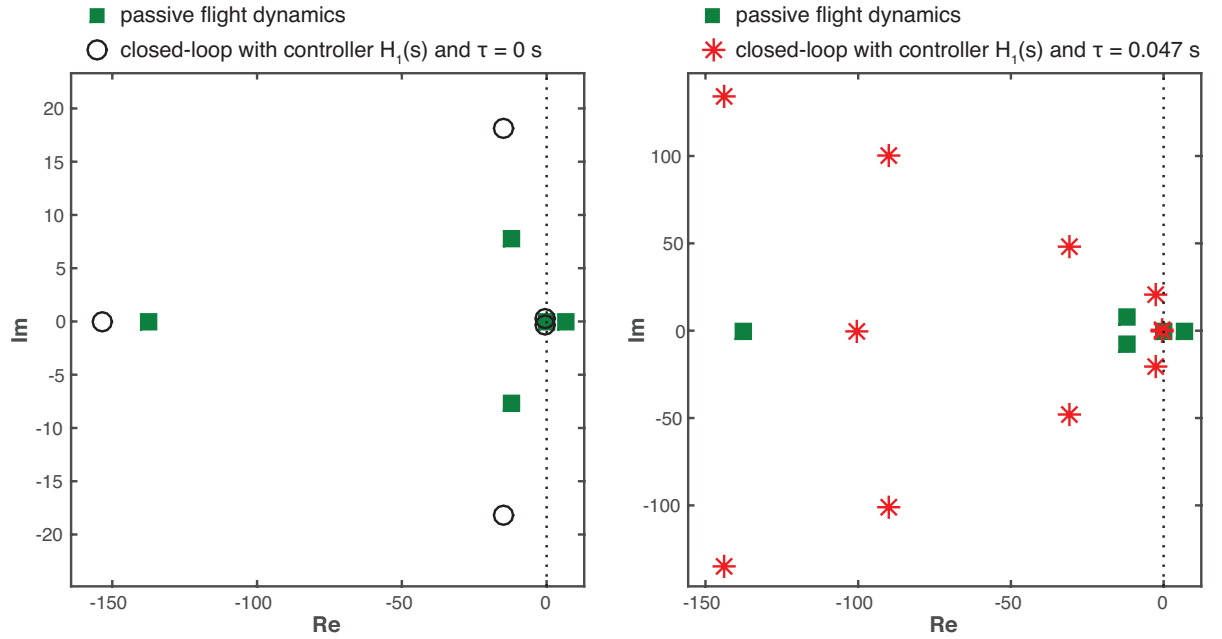


**Figure 5.13:** Root locus plots for the lateral flight dynamics. Both graphs show the eigenvalues of the passive flight dynamics (green squares) representing a slow, unstable divergence; a slow, stable oscillation; and a fast, stable subsidence mode. The eigenvalue in the origin is generated by adding the yaw angle  $\psi$  as a fifth state variable. The black circles in the left graph are all located in the left plane and show that the PI-controllers of  $H_1(s)$  render the system asymptotically stable for  $\tau = 0$  s. The red stars in the right graph are all located in the left plane and show that the PI-controllers of  $H_1(s)$  with a time delay  $\tau = 0.047$  s also render the closed-loop lateral flight dynamics asymptotically stable. The third order Padé approximation of the time delay introduces three additional eigenvalues per response moment. Hence, six red stars in the right plot are assigned to the approximation of the time delay.

The eigenvalue of the unstable divergence merges with the eigenvalue in the origin which has been generated by adding  $\psi$  as a fifth state variable. These two eigenvalues merge to form a stable oscillatory mode with  $\lambda = -0.29 \pm 0.33i$ . Also, the controller increases the frequency of the stable oscillatory mode from 1.23 Hz to 2.89 Hz. When I include a time delay of 0.047 s, the PI-controllers still make the closed-loop system asymptotically stable, as shown in the right root locus plot of figure 5.13. The right-most eigenvalues of the closed-loop system are located at  $\lambda = -0.30 \pm 0.38i$ . The third order Padé approximation introduces three eigenvalues per moment output of the system. Hence, it introduces six new eigenvalues, all of which are in the left plane of the root locus plot. Although the unstable divergence is stabilised (it still merges and transforms into a stable oscillatory mode), the eigenvalues of the slow, stable divergence and the eigenvalue of the stable oscillatory mode have moved to the right, indicating that the time delay has a destabilising effect. A sensitivity analysis as has been performed for the longitudinal flight dynamics is made much more complicated by the fact that we have two outputs, each of which contains four feedback gains.

In the second step, I analyse the performance of the PI-controllers of  $H_2(s)$ . These controllers had been derived from the responses to stimuli  $r$  (rotation about the vertical z-axis) and  $p'$  (rotation about the longitudinal x'-axis). Unlike above, this closed-loop system with  $H_2(s)$  and without time delay is not stabilised (left root locus plot in figure 5.14). This is because the real component of the unstable divergence mode remains positive. The stable oscillatory mode also transforms the original value of  $\lambda = -12.17 \pm 7.73i$  into two monotonic modes which are difficult to locate without sensitivity analysis. The right root locus plot in figure 5.14 shows that including the time delay of  $\tau = 0.060$  s does not stabilise the closed-loop lateral flight dynamics.

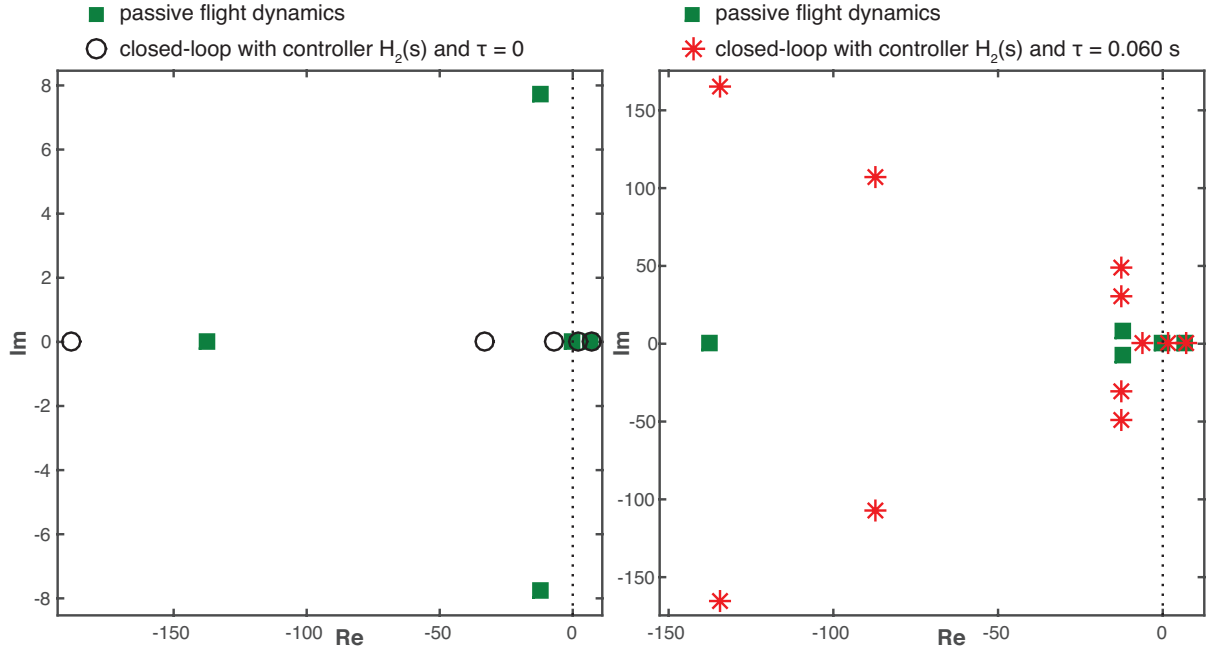


**Figure 5.14:** Root locus plots for the lateral flight dynamics. Both graphs show the eigenvalues of the passive flight dynamics (green squares) representing a slow, unstable divergence; a slow, stable oscillation; and a fast, stable subsidence mode. The eigenvalue in the origin is generated by adding the yaw angle  $\psi$  as a fifth state variable. The black circles in the left graph are not all located in the left plane and show that the PI-controllers of  $H_2(s)$  render the system unstable for  $\tau = 0$  s. The red stars in the right graph are not all located in the left plane and show that the PI-controllers of  $H_2(s)$  with a time delay  $\tau = 0.060$  s do not render the closed-loop lateral flight dynamics stable. The third order Padé approximation of the time delay introduces three additional eigenvalues per response moment. Hence, six red stars in the right plot are assigned to the approximation of the time delay.

## 5.4 Discussion

Using the measured morphological and inertial data I redimensionalised the system matrices  $\mathbf{A}_{\text{longitudinal}}$  and  $\mathbf{A}_{\text{lateral}}$ . I applied the eigenvalue decomposition to these two system matrices in order to describe the stability of the passive flight dynamics, i.e. the stability of the uncontrolled system. This showed that *M. sexta* have two inherently unstable

modes of motion, both of which require a control signal to maintain stable flight condition. First, there is a longitudinal unstable oscillation which entails the fore-aft motion coupled with a pitching motion. Second, there is a lateral unstable divergence which couples the sideslip and roll motion. The stability analysis of the closed-loop system showed that the unstable longitudinal mode of motion is not stabilised by the vision-based flight control model  $H_{M,q}(s)$ . A sensitivity analysis showed that the instability is strongly driven by the time delay of the integral feedback of angular position. But if I simulate the active pitch rate damping caused by fast mechanosensory feedback,  $H_{M,q}(s)$  does stabilise the longitudinal flight dynamics. The lateral unstable mode of motion is stabilised by the control model  $H_1(s)$ , but it is not stabilised by the control model  $H_2(s)$ . For MIMO systems, the interactions between the multiple control gains get convoluted very quickly. Hence, compared to the sensitivity analysis for the longitudinal SISO system, a more sophisticated sensitivity analysis would be required for the lateral MIMO system.

One factor that may influence the outcome of the stability analysis is the use of linearised and time-invariant flight dynamic models that are based on wingbeat-cycle-averaged forces and moment. These models are valid for insects with wingbeat frequencies that are at least an order higher than its highest natural frequency of motion, i.e. in species where the wingbeat frequency does not interfere with the natural frequencies of the system [75]. The redimensionalised flight dynamic models predict longitudinal and lateral oscillatory modes of motion with periods of 10 and 19 wingbeats, respectively (tables 5.3 and 5.5). I therefore expect the wingbeat-cycle-averaged models to offer a reasonable approximation of the flight dynamics of *M. sexta*. Zhang et al. [34] [35] compared the analytical predictions of these linearised models for *M. sexta* with the results of simulations that couple the rigid-body equations of motion with the fluid dynamic Navier-Stokes equations. They found that the simulations matched the analytical results of the model

quantitatively for the longitudinal flight dynamics, but only qualitatively for the lateral flight dynamics. According to those studies, the aerodynamic derivatives in  $\mathbf{A}_{\text{lateral}}$  are qualitatively correct but are likely to differ in a model where the forces and moments are not wingbeat-cycle-averaged.

The modes of motion that are stabilised by  $H_1(s)$  and  $H_{M,q}(s)$  are asymptotically stable. Hence, the disturbance motion will drop to zero and the system will converge to equilibrium state. But they are only stable by a small margin. This has already been found in the stability analysis of the visual-abdominal response in *M. sexta* [41]. This small stability margin illustrates the compromise between stability and manoeuvrability. Too much stability is detrimental to manoeuvrability, and similarly, not enough stability is detrimental to controllability. The control model for the responses to  $r$  and  $p'$ , i.e.  $H_2(s)$ , may only function in combination with a faster sensory modality or for a different range of stimulus parameters. As mentioned by Elzinga et al. [74], yaw is already passively stable. Therefore, rate damping from inertia feedback seems unnecessary, unless if it enables the visual system to operate at a larger gain and hereby allowing for a faster vision-based response.

The question remains: In what way does visual feedback complement the rapid feedback from mechanosensors? Does optic flow indicate motion about axes along which inertia sensing is not accurate enough? Inertia sensors are potentially limited by their activation frequency and the plane in which they are free to oscillate. Inertia sensors work by oscillating a mass in a plane perpendicular to the direction of interest. Because of the need of oscillating in a particular plane, the inertia sensor may not be able to cover a large enough range and therefore, the visual system provides significant and non-redundant feedback. Alternatively, the visual feedback may be sufficient if the stimuli had included a horizon, i.e. instead of having a uniform sine grating across the whole sphere, I could

have used a brighter top hemisphere. This would provide an additional cue for the moth to estimate its attitude and motion and hence, would enrich the visual feedback and potentially improve the system stability.

## **5.5 Conclusion and outlook**

This chapter concludes the experimental work performed with the data collected from tethered experiments. From this chapter, I conclude that visual feedback is sufficient to stabilise disturbances associated with rotational stimuli about the horizontal roll and dorso-ventral axes, but is insufficient to stabilise disturbances associated with rotational stimuli about the pitch axis, vertical yaw axis, and longitudinal body axis. This holds for the range of stimulus parameters presented in this study. Hence, either the models are wrong (for instance, I could apply another method to fit MIMO controllers) or they are incomplete (for instance, I could account for a non-linear component of the motion vision pathway or include sensory feedback from other modalities). The finding that vision is sufficient to stabilise some modes of motion does not rule out the possibility of other sensory modalities contributing to flight stability.

## Chapter 6

# Free flight responses to yaw stimuli

This chapter analyses the responses of free flying *M. sexta* to visual yaw stimuli. The stimuli comprised of a step impulse, meaning that the moth was exposed to a sudden onset of panoramic motion around the vertical axis of the flight arena. The apparent motion had a constant angular velocity of either  $80^\circ/\text{s}$ ,  $120^\circ/\text{s}$ , or  $160^\circ/\text{s}$ . The behavioural responses were recorded with high-speed videography and were analysed using photogrammetric reconstruction. The initial aim was to track the wingbeat kinematics and to determine the potential roll, pitch and yaw moment responses from the reconstructed 3D motion. But the automatic shape-carving procedure which is used to automatically track the moth's kinematics does not perform as well as it does for species with transparent wings [76] and is made complicated by the fact that the moth's wings obscure the head in some frames (i.e. the body location cannot be automatically determined). Hence, in this chapter I estimate the time delay and the roll and yaw moment responses of the free flying moths and compare them to the corresponding values measured in the tethered experiments. This comparison is performed because tethered experiments might not reflect the free flight behaviour, and this approach allows us to validate some of the model predictions

made using tethered-flight data in earlier chapters against free-flight data.

## 6.1 Material and methods

### 6.1.1 Animals

The experiments were performed using 10 male *M. sexta* within 1-4 days post-eclosion. The pupae and the moths were kept on a 12:12 light-dark cycle in an controlled environment of 25°C and 40-50% humidity. The moths were kept on a diet of sugar water.

### 6.1.2 Visual stimuli and data acquisition

For the experiments, the moths were taken from the raising chamber which was illuminated by an LED (simulating moonlit conditions at 0.25-4 lx) and gently put into the sphere (2.5-4 lx) of the virtual reality flight simulator (figure 6.1, A). The acrylic sphere measured 1 m in diameter and was painted with a transmissive opaque coating (Goo Systems Ltd, Rear Projection Screen Goo). A flower-like feeder was placed at the end of a translucent rod at the level of the sphere's equator so that the hovering moth was roughly located at the centre of the sphere (figure 6.1, C). The artificial flower consisted of a yellow cross which was made from electrical insulation tape applied across a 7x7 cm translucent plate. The translucent feeder was filled with sugar solution. The temperatures in the lab environment varied between 25-27°C.

The basic pattern of the stimulus is a sinusoidal grating with a constant spatial frequency of 0.05 cycle/° (equivalent to that used in the tethered experiments). When the moth was inserted, the sphere had a still image projected onto it. Once the moth presented a steady hover in front of the feeder, the pattern changed from a still image to a

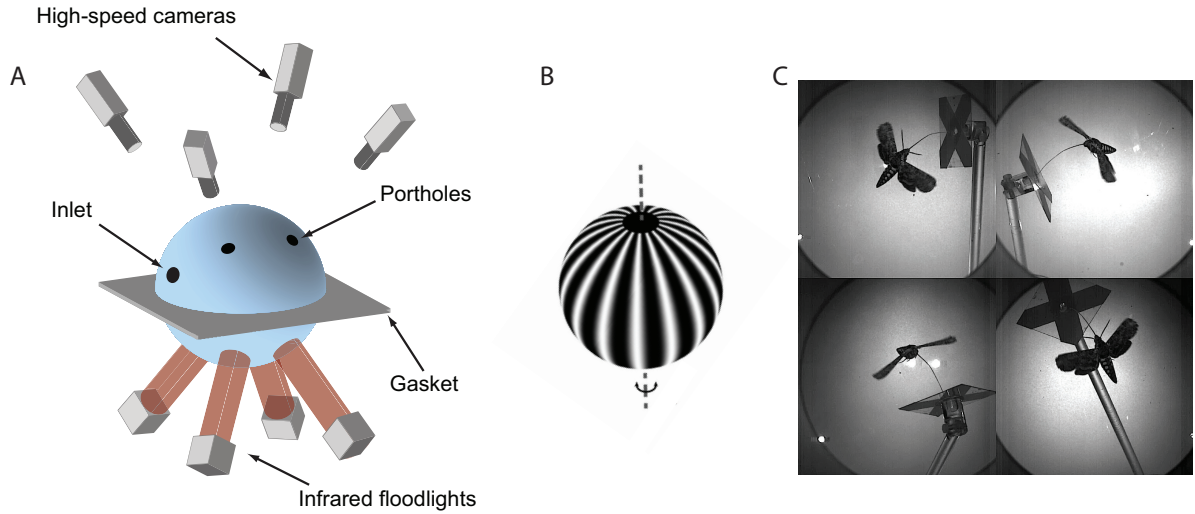


**Figure 6.1:** (A) Schematic of the free flight arena, including four high-speed cameras, four infrared floodlights that created the backlight, and an acrylic sphere onto which the yaw stimuli were projected. (B) Wide-field sinusoidal gratings rotated around the vertical axis of the flight arena to simulate apparent yaw motion of constant velocity. (C) View from the four high-speed cameras onto the moth which is feeding from the dummy flower. This imagery was used for photogrammetric reconstruction of the head position.

step impulse, whereby the pattern moved to either the left or the right hand side with a constant yaw velocity of either  $80^\circ/\text{s}$ ,  $120^\circ/\text{s}$  or  $160^\circ/\text{s}$  (figure 6.1, B). The angular velocities correspond to values for which I expected a strong, monotonic yaw response (see figure 3.8). Each stimulus was presented for 2-3 seconds and in most cases the moth swirled around the sphere before landing at the bottom. Whilst the recordings were being saved, the projectors were turned off, leaving the moth in the sphere at 0.2-0.4 lx for roughly 15 minutes. For each stimulus that was selected, the moth experienced the stimulus once as a left yaw turn and once as a right yaw turn with the same angular velocity. Each moth was exposed at least to one stimulus and at most to two stimuli. Stimuli of the same angular velocity were presented at a minimum of 30 minutes apart.

The sine gratings were rendered in MATLAB (MATLAB v. 7.4, The Mathworks Inc.,

Natick, MA, USA) and uploaded to two synchronised, digital projectors which were fitted with DC lamps (LT170, NEC, Japan) and retrofitted with micromirror chipsets (ALP-2, ViALUX, Chemnitz, Germany). The images measured 1024x768 pixels and were projected at a rate of 144 Hz with 8 bit greyscale. Two neutral density filters (62 mm HMC NDX2 and NDX4, HOYA, Japan) were screwed onto each projector in order to simulate crepuscular light conditions (2.5-4 lx). This corresponds to twilight conditions and matches the settings used in previous studies with *M. sexta* [41], [46]. Backlight was generated by four infrared floodlights that illuminated the sphere from four corners below the sphere (figure 6.1, A). In order to illuminate the moth from the top, I used custom-made infrared LED spotlights. Four synchronised Photron SA3 cameras (Photron Ltd) were equipped with 100 mm F2.8 macro lenses (Kenko Tokina Co., Ltd.). Images were recorded at 2000 Hz over a period of 1.363 s and with a resolution of 1024x1024 pixels. The shutter speed was 0.5 ms, leading to slightly blurred images of the wingbeat. The cameras were triggered manually shortly before the onset of the moving stimulus. Using a centre trigger, I recorded 0.401 s prior and 0.962 s post-trigger in order to capture the moth's behaviour before and after the step impulse. For the temporal alignment, I recorded the trigger signal for the high-speed cameras, the trigger signal for the stimulus onset, and the signal for the frame projection at a sampling rate of 10 kHz.

### 6.1.3 Photogrammetric reconstruction of the head position

The cameras were calibrated using custom-written software in MATLAB to produce optimal estimates of the spatial coordinates of points on a two-dimensional calibration grid, presented at a range of positions and orientations [77]. For the analysis of the response behaviour, a selection of 30 video sequences were down-sampled to 50 Hz, i.e. I sampled the head position twice per wingbeat period. For each trial, I used the custom-written

software in MATLAB to define the position of the feeder and to track the moth's head for the duration of the whole recording. The 3D coordinates of the head were transformed into a spherical coordinate system with its origin at the feeder. Hence, the position of the head relative to the feeder is defined by its azimuth  $\gamma$  (i.e. latitude or horizontal angle), its elevation  $\xi$  (i.e. longitude or vertical angle), and its radial distance  $R$ . I fitted a quintic smoothing spline to  $\gamma$ , with a tolerance factor calculated from the residuals of fitting a third-order Butterworth filter with a cut-off frequency of 20 Hz. The 20 Hz filter frequency was selected to minimise contamination of the head kinematics by the wingbeat. This spline was then resolved at the time points of the initial recording of 2000 Hz for which I had determined the frame of the stimulus onset with an uncertainty of  $1.2 \pm 0.3$  ms. Subsequently,  $\gamma$  was set to 0 at the time point of stimulus onset.

## 6.2 Analysis of the time delay and the moment responses to yaw stimuli

In the first column of figure 6.2 we see the azimuth for each trial at a precision of 50 Hz, but the interpolated spline is plotted with a resolution of 200 Hz. The time point  $t=0$  is the time point of the stimulus onset and the reference point for  $\gamma$ , i.e.  $\gamma(t=0)=0$ .

In the first column of figure 6.2,  $\gamma$  is averaged across 14 trials for stimuli of  $80^\circ/\text{s}$ , across 10 trials for stimuli of  $120^\circ/\text{s}$ , and across 6 trials for stimuli of  $160^\circ/\text{s}$ . The mean azimuth was then fitted with a quintic smoothing spline, with a tolerance factor calculated from the residuals of fitting a third-order Butterworth filter with a cut-off frequency of 20 Hz. The second column in figure 6.2 shows the first time-derivative of this spline, i.e. the rate of change  $\dot{\gamma}$ . The time delay of the response is defined as the time difference between the onset of the stimulus at  $t=0$  and the time point where the moths begin to compensate for

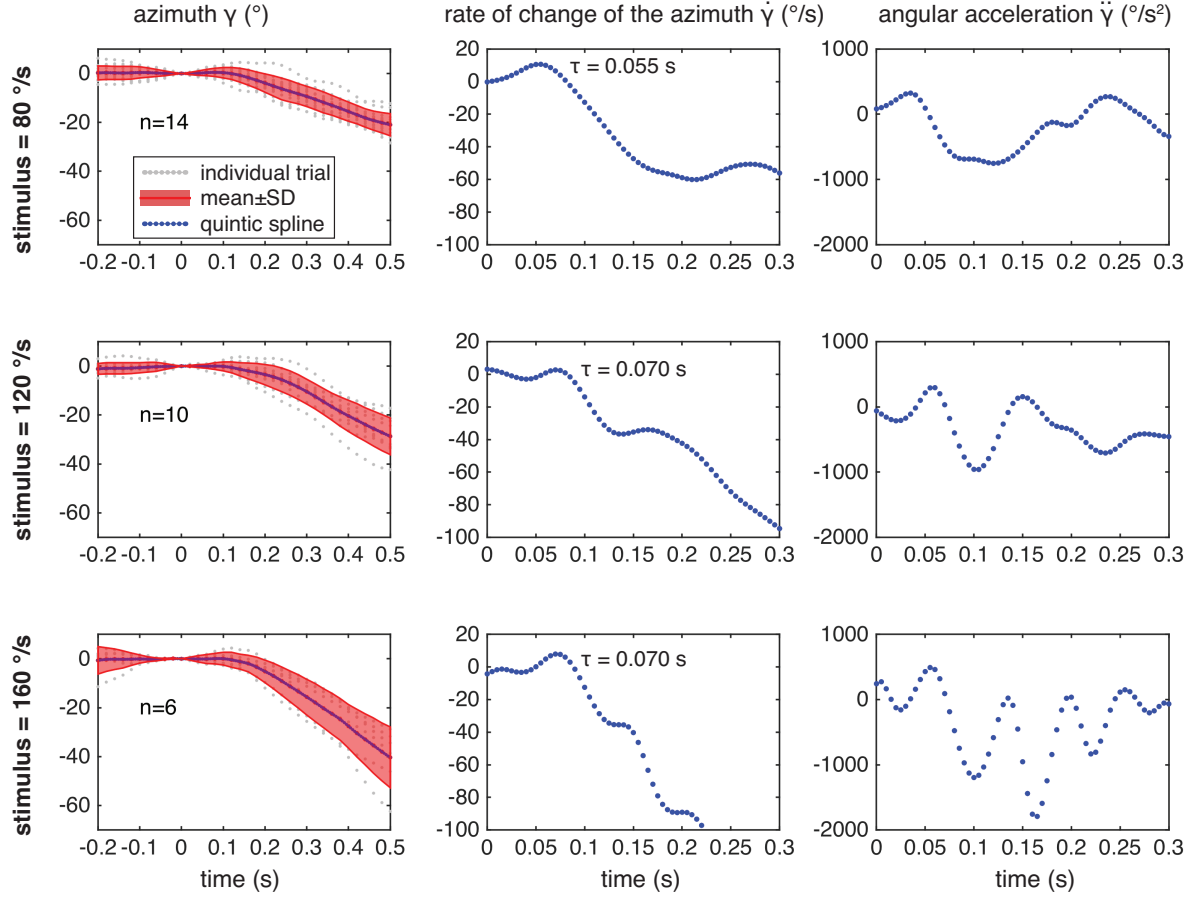


**Figure 6.2:** Position and movement of the moth's head in response to the sudden onset of a yaw stimulus with a constant velocity of 80°/s (1st row), 120°/s (2nd row), and 160°/s (3rd row).  $\gamma$  is the azimuth, i.e. the horizontal angle between the feeder and the moth's head. The reference for  $\gamma$  is the time point of stimulus onset, i.e.  $\gamma(t=0)=0$ . The first column illustrates the azimuth  $\gamma$  for each individual trial (grey), the corresponding mean  $\pm$ SD (red), and the mean approximated by a quintic spline (blue).  $n$  indicates the number of trials recorded per stimulus velocity. The second column illustrates the first time derivative of the quintic spline, i.e. the rate of change  $\dot{\gamma}$  of the azimuth.  $t$  indicates the time delay of the response. Hence, it is the time point above which the direction of the response is consistent with the direction of the stimulus. The third column illustrates the second time derivative of the quintic spline, i.e. the angular acceleration  $\ddot{\gamma}$ .

image speed, i.e. the time point above which the head consistently moves in the direction of the stimulus. The rate of change  $\dot{\gamma}$  exhibits a distinct peak at the point where the direction of motion changes from one that opposes the stimulus to one that moves in the direction of the stimulus (2nd column in figure 6.2). For stimuli of  $80^\circ/\text{s}$ , the time delay is 0.055 s. For stimuli of either  $120^\circ/\text{s}$  or  $160^\circ/\text{s}$ , the time delay is 0.070 s. This difference in the response time could be a consequence of the moth's habit to stabilise its position in space whilst feeding from a flower. Hence, as the panoramic rotation sets in, the moth is confronted with two reflexes at the same time: one is to maintain the distance to the flower, and the other is to compensate for the apparent rotational drift. Farina et al. [78] and Kern et al. [79] report that for relatively large flowers and for shorter distances from the flower, *Marcoglossum stellatarum* favour the distance stabilisation to the flower over the compensation of the motion imposed by moving striped patterns. Figure 6.3 shows the elevation  $\xi$  and the distance  $R$  of the moth's head relative to the feeder at the time of the stimulus onset ( $t=0$ ) for the three different stimulus velocities.

The left graph of figure 6.3 shows that on average, the moth's head was  $\sim 4^\circ$  above the flower when exposed to yaw velocities of  $80^\circ/\text{s}$ , whereas on average, the moth's head was  $\sim 20^\circ$  above the flower when exposed to yaw velocities of  $120^\circ/\text{s}$  and  $160^\circ/\text{s}$ . Consistent with this, the right graph of figure 6.3 shows that the mean distance of the moth's head from the flower grew slightly larger when the stimulus had a higher angular velocity. The same sized dummy flower was used for all experiments. Hence, it appears that the time delay is larger for stimuli at which the moths were located further away and above the flower, i.e. where the flower occupied a smaller amount of the visual field and where the object of interest was located in the lower hemisphere of the visual field. Coming back to a point discussed in chapter 3, this difference in delay could reflect regional differences in motion sensitivity in different parts of the moth's visual field [80] [10].

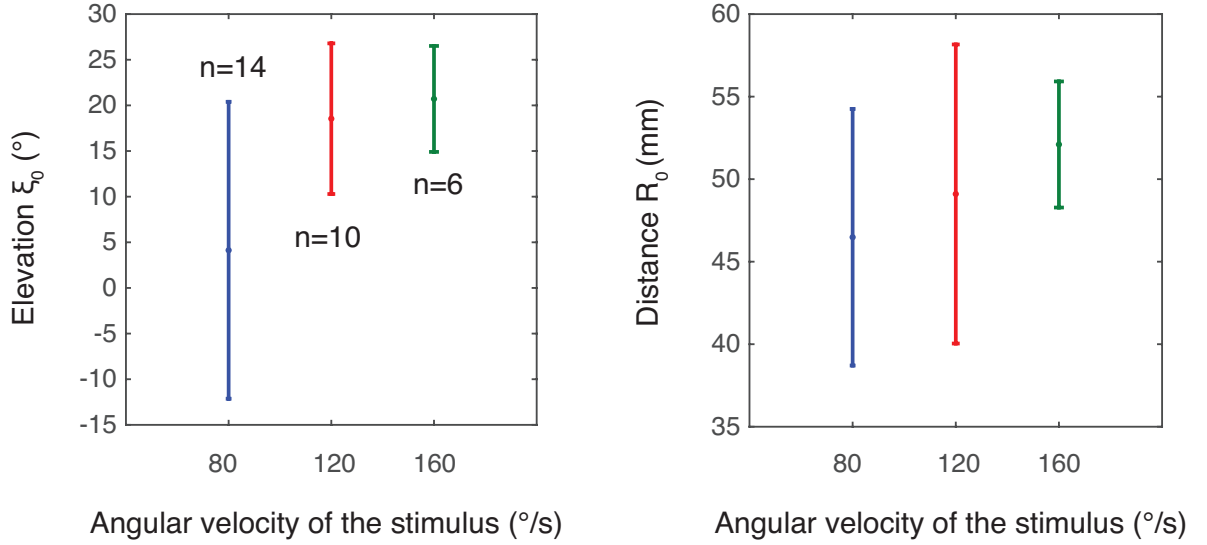


**Figure 6.3:** Location of the moth's head relative to the feeder at the onset of the stimulus ( $t=0$  s). Each datapoint indicates the mean $\pm$ SD.  $n$  indicates the number of trials averaged for each stimulus. The left graph shows that on average, the moth's head was  $\sim 4^\circ$  above the feeder when exposed to yaw velocities of  $80^\circ/\text{s}$ . Whilst on average, the moth's head was  $\sim 20^\circ$  above the feeder when exposed to yaw velocities of  $120^\circ/\text{s}$  and  $160^\circ/\text{s}$ . The right graph shows that the distance of the moth's head from the feeder was slightly larger when the stimulus had a higher angular velocity. The same sized dummy flower was used for all experiments. The location and the relative size of the flower in the moth's field of view could cause differences in the response behaviours.

As shown in the 2nd column of figure 6.2, the rate of change  $\dot{\gamma}$  appears constant for a stimulus of  $80^\circ/\text{s}$  whereas for stimuli of  $120^\circ/\text{s}$  and  $160^\circ/\text{s}$ , the response slows down at  $\sim 0.06$  s after the onset of the response. I estimated the mean acceleration  $\ddot{\gamma}$  of the head by fitting a regression line to the first 0.05 s after the onset of the response (i.e. to the 10 data points following the peak of  $\dot{\gamma}$ ). The estimated values for the angular acceleration  $\ddot{\gamma}$  are given in table 6.1. The acceleration increases for larger angular velocities of the stimulus, but it does not double for a doubling in the stimulus velocity. Next, I use the estimates of the angular acceleration  $\ddot{\gamma}$  in combination with the equation of motion in

order to estimate the yaw and roll moment responses that cause the moth's acceleration. Based on eyeballing the moth's motion in the high-speed videos, I assume that the moth is accelerating on a planar arc around the feeder and that the moth's roll and pitch rates are negligible ( $p = q = 0$ ). Hence, I insert the estimated values of  $|\ddot{\gamma}|$  into the linearised equations of motion (equations 6.1 and 6.2).

$$N_{acc} = \ddot{\gamma} \frac{I_x I_z - I_{xz}^2}{I_x - \frac{I_{xz}^2}{I_z}} \quad (6.1)$$

$$L_{acc} = -\ddot{\gamma} \frac{I_x I_z - I_{xz}^2}{I_x - \frac{I_{xz}^2}{I_z}} \cdot \frac{I_{xz}}{I_z} \quad (6.2)$$

The estimated response moments  $N_{acc}$  and  $L_{acc}$  that generate the angular acceleration  $\ddot{\gamma}$  are given in table 6.1.

**Table 6.1:** The angular yaw acceleration of the moth's head  $\ddot{\gamma}$  is derived from the 3D reconstruction of the head position relative to the feeder.  $\ddot{\gamma}$  is then used to calculate the response moments  $N_{acc}$  and  $L_{acc}$  that cause the moth to accelerate on a planar arc around the feeder.

|                                       | 80°/s  | 120°/s | 160°/s |
|---------------------------------------|--------|--------|--------|
| $ \ddot{\gamma} $ (°/s <sup>2</sup> ) | 563    | 737    | 891    |
| $N_{acc}$ (N m)                       | 1.2e-6 | 1.5e-6 | 1.9e-6 |
| $L_{acc}$ (N m)                       | 8.5e-7 | 1.1e-6 | 1.3e-6 |

The moment responses to yaw stimuli in free flight consist of two components: one component which causes the moth's planar acceleration around the feeder, and a second component that is attributed to yaw rate damping (i.e. flapping counter torque) [81]. Springthorpe et al. [59] report a half-life (the time it takes for the insect to decelerate to half of its initial angular velocity) of the flapping counter torque of 0.7 wingbeats for *M. sexta*.

In order to compare the estimated values of the yaw and roll moment responses of the

## Chapter 6 Free flight responses to yaw stimuli

free flight responses with those measured in the tethered experiments (figure 3.8), I need to add the moment response components that are dampened by the interaction of the body and wings with the airflow to  $N_{acc}$  and  $L_{acc}$  in table 6.2.  $N_{acc}$  and  $L_{acc}$  correspond to the moment responses that generate the acceleration only, which explains why they are so much smaller than the values measured in the tethered experiment which contain the component that needs to be overcome before allowing the moth to accelerate (table 6.2). The moments  $N_{dampened}$  and  $L_{dampened}$  that the moths need to overcome due to aerodynamic damping are defined by the aerodynamic derivative in the system matrix  $\mathbf{A}_{lateral}$  (discussed in section 5.1). By resolving the third term in the third column of  $\mathbf{A}_{lateral}$  I find that the damping of the yaw moment response due to a unit change in angular rate is  $N_r = 1.62 \times 10^{-5}$  N m s. In order to get the yaw moment  $N_{dampened}$  with the units N m in table 6.2, I multiply  $N_r$  with the angular acceleration  $|\ddot{\gamma}|$  (table 6.1) integrated over the duration of 0.058 s (i.e. the time for which the moment is fully dampened, using 0.7 times the wingbeat period as half time).  $L_{dampened}$  is calculated using the second term in the third column of  $\mathbf{A}_{lateral}$ , with  $\dot{p}=0$  and with  $N = N_{dampened}$ . In order to get the moment in the units mN mm  $g^{-1}$ , I multiply the values of  $N_{acc}$  and  $L_{acc}$ , and  $N_{dampened}$  and  $L_{dampened}$  with  $10^6$  and divide them by the mean moth mass of 1.75 g to get the values presented in table 6.2.

The estimates of the total moment responses generated in the free flight responses are of the same order of magnitude as those generated in the tethered setup. Generally, the yaw moment is estimated larger than the measured yaw moment response, and the roll moment is estimated smaller than the measured roll moment response. Hence, the ratio of the response moments  $N/L$  is larger across all stimulus velocities for the free flight responses when compared to the ratio of the moment responses for the tethered experiments.

**Table 6.2:** Comparison of the yaw ( $N$ ) and roll ( $L$ ) moment responses of moths exposed to wide-field yaw stimuli in the free flight and in the tethered flight setup. All moments are normalised by the mean mass and are given in  $\text{mN mm g}^{-1}$ . From the high-speed video recordings of the free flight responses I derive the angular acceleration  $|\ddot{\gamma}|$  of the moths and calculate the moments that are generated to keep the moth accelerating ( $N_{acc}$  and  $L_{acc}$ ). I add to those the moments that need to be overcome due to aerodynamic damping effects ( $N_{dampened}$  and  $L_{dampened}$ ). The total estimated moment responses of the free flying moths are  $N$  and  $L$ . These responses are in the same order of magnitude than the measured moment responses in the tethered setup.

| stimulus velocity:      | 80°/s | 120°/s | 160°/s |
|-------------------------|-------|--------|--------|
| <i>free flight:</i>     |       |        |        |
| $N_{acc}$               | 0.69  | 0.86   | 1.09   |
| $N_{dampened}$          | 5.99  | 7.78   | 9.45   |
| $L_{acc}$               | 0.49  | 0.63   | 0.74   |
| $L_{dampened}$          | 3.79  | 4.96   | 5.99   |
| $N$                     | 6.67  | 8.63   | 10.53  |
| $L$                     | 4.28  | 5.59   | 6.73   |
| $N/L$                   | 1.56  | 1.54   | 1.56   |
| <i>tethered flight:</i> |       |        |        |
| $N$                     | 5.43  | 7.75   | 9.99   |
| $L$                     | 7.30  | 8.14   | 7.85   |
| $N/L$                   | 0.74  | 0.95   | 1.27   |

### 6.3 Discussion

In this chapter I exposed moths that were feeding in front of a dummy flower to sudden onsets of a panoramic yaw stimulus. The stimuli had a constant yaw velocity of 80°/s, 120°/s, or 160°/s. The responses show a stereotypic increase of  $\dot{\gamma}$  in the direction opposing the apparent yaw before generating a consistent angular rate in the direction of the stimulus. The time delay is 0.055 s for the lowest stimulus velocity 80°/s and increases to 0.070 s for the two larger velocities 120°/s and 160°/s. Under the assumption that there is no significant roll or pitch rate in the free flight responses, the estimated moment responses

## Chapter 6 Free flight responses to yaw stimuli

that generate the planar yaw acceleration around the feeder range between  $8.5\text{e-}7$  N m to  $1.3\text{e-}6$  N m for the roll moment response, and  $1.2\text{e-}6$  N m to  $1.9\text{e-}6$  N m for the yaw moment response.

The time delay matches well with those derived from the tethered experiments, i.e. those derived from phase responses to yaw stimuli in section 3.6 (0.066 s), and those fitted to the flight controllers in section 4.3 (0.077 s for the roll moment response to yaw stimuli  $H_{L,r}(s)$ , and 0.057 s for the yaw moment response to yaw stimuli  $H_{N,r}(s)$ ). Under the assumption that the same processing pathway is used to compensate for apparent yaw rotations, I did not expect the time delay to increase with stimulus velocity. Potential differences in the time delay could have arisen due to the lower luminance in the free flight experiments (4 lx instead of 10 lx used in the tethered experiments), due to the fact that the moth is flying, or due the competing reflexes of the moth to either maintain the distance to the flower or to compensate motion drift of the panoramic stimulus. I expect a more precise measurement of the time delay by resolving the wingbeat kinematics.

The analysis presented in this chapter provides strong evidence that the moment measurements and that the time delays I had derived from the tethered flight experiments are valid to model the free flight behaviour of *M. sexta*.

## Chapter 7

# Conclusion and outlook

The aim of this thesis was to assess the role of visual feedback in flight control and stabilisation in *M. sexta*. For this, I analysed the fundamental properties of the optomotor responses and fitted vision-based flight controllers to the empirical data. I then assessed the stability of the closed loop flight dynamics. This was done by combining the empirically derived flight control models with existing models of the flight dynamics. The conclusions I draw from the behavioural responses of tethered moths is validated by the free flight responses analysed in chapter 6.

The power spectra in chapters 3 and 4 show that below the wingbeat frequency, the response power is focused at the fundamental frequency of the stimulus. I therefore model the optomotor responses based on the assumption of quasi-linearity. This means that the system is characterised by analysing the response behaviour generated at the frequency of the stimulus only. The describing functions in chapter 3 provide evidence for the non-linear effect of stimulus amplitude: larger stimulus amplitudes typically lead to smaller magnitude responses and to a shallower roll-off in the phase response. I suggest this is caused either by a pure effect of amplitude (e.g. spatial anisotropy of EMDs,

## *Chapter 7 Conclusion and outlook*

or limited ability of gaze stabilisation), or by the sensitivity of the system to angular rates (e.g. temporal anisotropy of EMDs). The moment responses to yaw stimuli do not adapt with stimulus amplitude in the same way that the moment responses do for roll and pitch stimuli. I suggest that this significant behavioural difference is due to the degree of freedom of gaze stabilisation. Future work could provide evidence for this by tracking the head movements in response to roll, pitch or yaw stimuli. From chapter 4 onwards, I focus on the optomotor responses to stimuli with an amplitude of  $5^\circ$ . The total moment responses to longitudinal and lateral stimuli are best explained by linear, time delayed PI-controllers (i.e. controllers using proportional-integrative feedback relative to the angular rate of motion). The longitudinal controller which operates with a delay of 0.042 s superposes with the lateral control laws (figure 4.10). This spatial superposition of control laws predicts the response behaviour to stimuli that combine longitudinal and lateral motion. Conversely, the difference in time delay prevents the superposition of the two control laws for lateral stimuli with a time delay of 0.047 s and 0.060 s, respectively. Hence, the responses analysed in chapter 4 do not support the existence of a global vision-based flight controller that stabilises arbitrary lateral stimuli. One main finding is that the rotation axis has a substantial effect on the time delay of the optomotor response. This is interesting, because if the optomotor system has more than three pathways with different time delays, the system is underdetermined and therefore unidentifiable if its output is represented by only three independent moments. Future work could investigate the time delays in the motion vision pathway more closely. Because of the design of the two controllers  $H_1(s)$  and  $H_2(s)$  for the lateral stimuli, I suggest analysing the optomotor responses to rotation about an axis intermediate to x and z', and to rotation about an axis intermediate to -z and x'. It would be interesting to see whether those response time delays are significantly different to 0.047 s or 0.060 s, respectively. If not, then this

## Chapter 7 Conclusion and outlook

could indicate two distinct rotational patterns of motion that the visual system is tuned to. Also, the fitting process of the control models for the two-input, two-output systems  $H_1(s)$  and  $H_2(s)$  could be improved. For instance by implementing the Relative Gain Analysis (RGA) which detects inter-loop coupling of the control laws  $H_{L,p}(s)$ ,  $H_{N,p}(s)$ ,  $H_{L,r}(s)$  and  $H_{N,r}(s)$  [82]. In chapter 5, the control loop is closed by combining the vision-based flight controllers with the linearised flight dynamics of a hovering moth. The stability analysis shows that lateral disturbances about the x- and z'-axis are stabilised by a PI-controller and a time delay of 0.047 s. Conversely, lateral disturbances about the z- and the x'-axis are not stabilised by a PI-controller with a time delay of 0.060 s. Also, pitch stimuli are not stabilised by a PI-controller that operates with a time delay of 0.042 s. Although, if I simulate prior pitch rate damping, the empirically derived controller does stabilise the system, with a thin stability margin. Hence, the empirically derived vision-based flight controllers are sufficient to stabilise rotations about the x- or z'-axis, whereas they are insufficient or only complementary to feedback from other sensory modalities if the moth experiences rotations about the y-, z-, or x'-axis. A sensitivity analysis revealed that the time delay strongly drives an instability introduced by the integral feedback of angular position. Future work could assess whether this different performance of flight control models still holds if the visual stimuli includes an artificial horizon. The estimation of the moth's angular position relative to the horizon may modify the vision-based flight controller and may change the stability performance observed here. It would also be interesting to expand this model with knowledge of the dynamic and spatial range of body rotations for which proprioceptive feedback is provided.

This thesis concludes with three hypotheses and corresponding suggestions for future work: First, I hypothesise that the limited degree of freedom for gaze stabilisation causes

## *Chapter 7 Conclusion and outlook*

the different moment response behaviours for roll, pitch and yaw (observed in figure 3.8). This can be analysed in more detail by tracking head motion. Second, I hypothesise that the time delay has a substantial effect on the system because it prevents spatial superposition and because it causes visual feedback to be insufficient for stabilising disturbances about specific axes of rotation. The time delay is a key parameter to investigate in order to see whether the optomotor responses can indeed be fully identified. Future work could entail measuring optomotor responses for stimuli about other axes, and measuring optomotor responses for stimuli with a horizon. Third, I hypothesise that visual feedback is sufficient to stabilise some disturbances but it is insufficient to stabilise others. Hence, it would be interesting to explore whether visual feedback stabilises the system for rotations about axes where proprioceptive feedback (e.g. inertial feedback from the antennae, wings or abdomen) may be prevented or unreliable. For instance, how does the optomotor time delay vary with the amount of proprioceptive feedback that can be provided?

Based on the thorough sampling of the optomotor responses I was able to establish new methods for studying the mechanisms underlying the motion vision pathway. This study also illustrates the importance and the caveats of implementing multiple-input, multiple-output controllers with a time delay in order to model a biological flight response behaviour. Overall, this thesis demonstrates the usefulness of applying a systems engineering approach to study the variation in flight control mechanisms and the functionality of sensorimotor control.

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# Appendix A

## Appendix chapter 2

### A.1 Motion patterns for double-sine waveforms

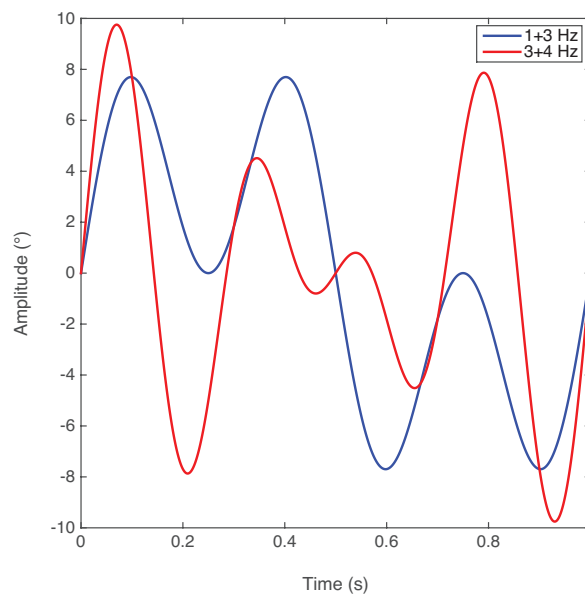


**Figure A.1:** The amplitude of motion for the double-sine waveforms, combining 1 and 3 Hz (blue), and 3 and 4 Hz (red).

## A.2 A more detailed explanation of the data processing

- The voltage measurements are transformed to forces (mN) and moments (mN mm) by the calibration matrix. Generally, the amplitudes of the moment responses (100-300 mN mm) are an order higher than those of the force responses (5-10 mN).
- The measured forces and moments are transformed to the centre of mass (CoM). The location of the CoM was estimated separately for each individual moth. To do this, I clipped off the wings from the frozen body, and suspended the moth from a pin at various pivot points on the moth's body and appendages (figure A.2). I took images of the moth's body next to which I had hung a plumb line to evaluate the alignment of the suspended body relative to gravity. Using MATLAB (MATLAB v. 7.4, The Mathworks Inc., Natick, MA, USA), I identified the intersection of the plumb line and the body axis and aligned and digitally overlaid these images to determine the average location of the CoM in the sagittal plane of each moth. The CoM was evaluated in percentage of body lengths from the head (for  $n=26$ ,  $0.44 \pm 0.01$ , mean  $\pm$  SEM). Side-on photographs were then used to estimate the distance between the force transducer and the CoM (figure A.3).



**Figure A.2:** Having clipped off the wings from the frozen body, images were taken from the moth as it was suspended from a pin at various pivot points on the moth's body and appendages, next to a plumb line.

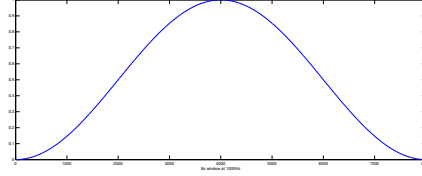


**Figure A.3:** Once the centre of mass was evaluated, a side-on photograph is used to estimate the distance between the force transducer and the centre of mass for a particular moth.

- The measured signals are then detrended, i.e. the linear trend which may be caused by a thermal unbalance in the sensor is removed.
- We loop through sections of the time domain signal and apply the chirp z-transform (CZT) to convert the signal into the frequency domain. The CZT delivers the input spectrum ( $P_{xx}$ ), output spectrum ( $P_{yy}$ ) and cross power spectrum ( $P_{xy}$ ), the frequency response function  $H$  and the coherence  $\gamma^2$  across a frequency spectrum of 0 to 60 Hz, with a resolution of 0.1 Hz. The CZT implemented window averaging (Welch's method) has the advantage of providing an improved frequency resolution and accuracy over the usual fast Fourier transform [49].

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- Both the stimulus and measured time domain signals are windowed into 8 s sections with 80% overlap ( $\sim 40$  windows)
- Each window is detrended and then multiplied with a Hanning window



- Each 8 s window of measured data is then separately transformed into the frequency domain, delivering  $Fxx$  and  $Fyy$ . Hence, a complex number is evaluated for each window.  $r$  corresponds to the amplitude and  $\varphi$  is the phase of the measured signal.

$$Fxx = r_{stim}$$

$$Fyy = r_{resp}e^{i\varphi}$$

- The cross-correlation  $Pxy$  and auto-correlations  $Pyy$  and  $Pxx$  are evaluated for each window:

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$$\begin{aligned}
 Pxy &= \frac{\bar{F}xx \cdot Fyy}{\text{window power}} = r_{stim}r_{resp}(\cos\varphi + i\sin\varphi) \\
 Pxx &= \frac{\bar{F}xx \cdot Fxx}{\text{window power}} = r_{stim}^2 \\
 Pyy &= \frac{\bar{F}yy \cdot Fyy}{\text{window power}} = r_{resp}^2
 \end{aligned}$$

- $Pxy$ ,  $Pyx$  and  $Pxx$  are then averaged across  $\sim 40$  windows

$$\begin{aligned}
 Pyy &= \frac{\sum Pyy}{\text{number of windows}} \\
 Pxx &= \frac{\sum Pxx}{\text{number of windows}} \\
 Pxy &= \frac{\sum Pxy}{\text{number of windows}}
 \end{aligned}$$

- The frequency response  $H$  and coherence  $\gamma^2$  are calculated for each individual trial. There are various formulae that can be used to calculate the transfer function  $H$  and we chose the formula that minimises the effect of noise in the measured output.

$$H = \frac{Pxy}{Pxx} \tag{A.1}$$

$$\gamma^2 = \frac{|Pxy|^2}{Pxx \cdot Pyy} \tag{A.2}$$

- As shown in equation A.2, the coherence depends on the input spectrum  $Pxx$ , the output spectrum  $Pyx$  and the cross-power spectrum  $Pxy$ . Each of these three values represent a mean, averaged across  $\sim 40$  windows of the time-domain signal. For a

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periodic stimulus,  $Pxx$  will remain constant.  $Pyy$  will change if the response amplitude changes between windows and if measurement noise is not averaged out across windows (i.e. if noise is bound to the stimulus frequency rather than being random noise).  $Pxy$  is affected by the stimulus amplitude, the response amplitude, the relative phase and measurement noise. Hence, for a periodic input,  $Pxy$  will vary only with noise and with either an inconsistent phase or response amplitude. Nonlinearities in the response will not affect  $Pyy$  nor  $Pxy$  as these values are evaluated at the stimulus frequency only. Ideally, the stimulus would contain multiple temporal frequencies (e.g. white noise) and the coherence would be evaluated at multiple frequencies in which case non-linear response dynamics would be detected [50].

- Normalise the frequency response by the moth's mass
- From the normalised frequency response function we derive the magnitude and phase response at the fundamental oscillation frequency of the corresponding trial.

$$\text{magnitude} = \sqrt{\text{real}(H)^2 + \text{imag}(H)^2} \quad (\text{A.3})$$

$$\text{phase} = \text{atan}\left(\frac{\text{imag}(H)}{\text{real}(H)}\right) \quad (\text{A.4})$$

$$H = \text{magnitude} \cdot e^{j \cdot \text{phase}} \quad (\text{A.5})$$

## Appendix B

### Appendix chapter 3

B.1 Power spectra and coherence for single-sine roll,  
pitch and yaw stimuli

B.2 AICc analysis of the magnitude and phase  
responses to roll, pitch and yaw stimuli

## Appendix B Appendix chapter 3

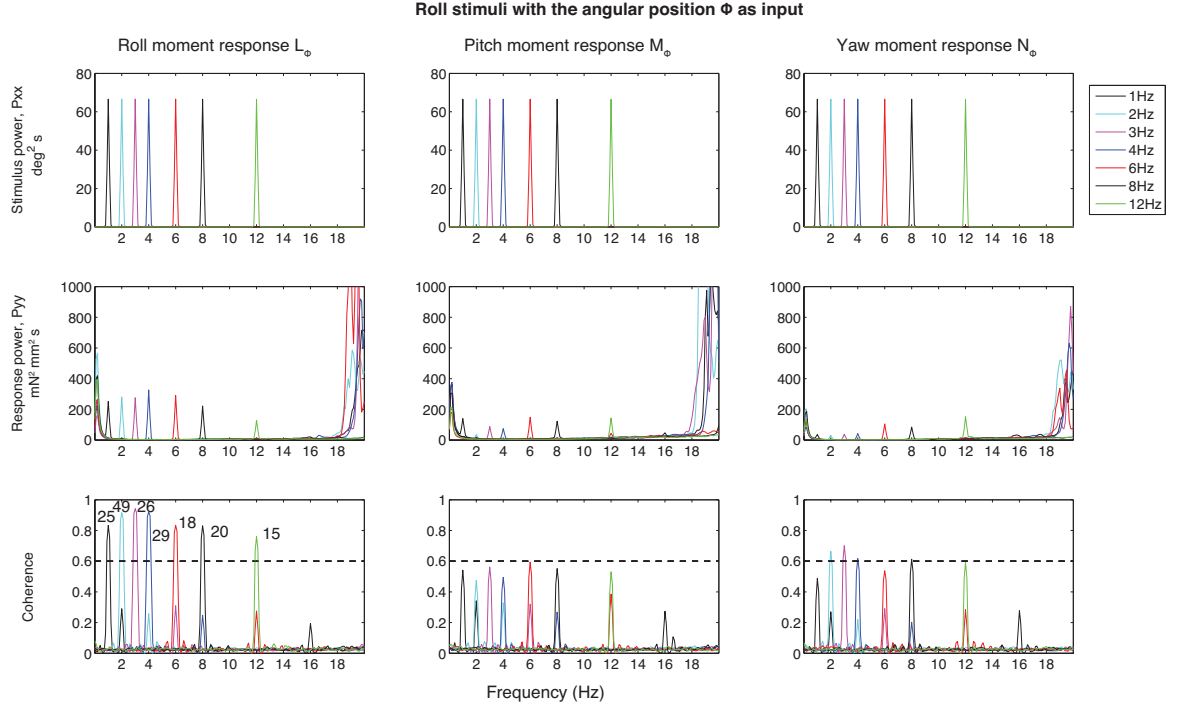


**Figure B.1:** Frequency spectra for seven single-sine roll oscillations of 5° amplitude, ranging from 1 Hz to 12 Hz. The top row show the power spectrum of the stimulus. The second row shows the power spectrum of the response. The third row shoe the coherence, i.e. the amount of power of the stimulus that is linearly transferred to the response. Each colour relates to one individual stimulus. The responses are plotted across a frequency spectrum of 0 to 20 Hz on a linear scale. The numbers in the coherence plot indicate the number of trials averaged for that specific stimulus. Below the wingbeat frequency at  $\sim 23$  Hz, the bulk response power is provided at the fundamental oscillation frequency.

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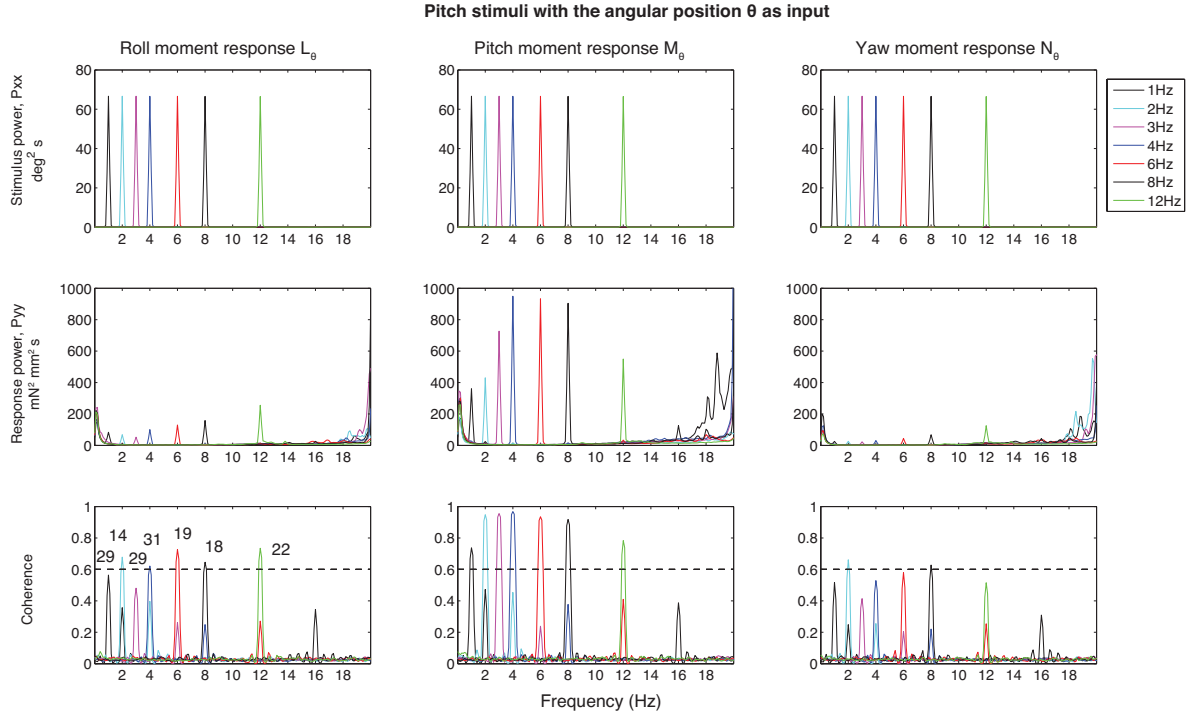


**Figure B.2:** Frequency spectra for seven single-sine pitch oscillations of 5° amplitude, ranging from 1 Hz to 12 Hz. The top row show the power spectrum of the stimulus. The second row shows the power spectrum of the response. The third row shoe the coherence, i.e. the amount of power of the stimulus that is linearly transferred to the response. Each colour relates to one individual stimulus. The responses are plotted across a frequency spectrum of 0 to 20 Hz on a linear scale. The numbers in the coherence plot indicate the number of trials averaged for that specific stimulus. Below the wingbeat frequency at  $\sim 23$  Hz, the bulk response power is provided at the fundamental oscillation frequency.

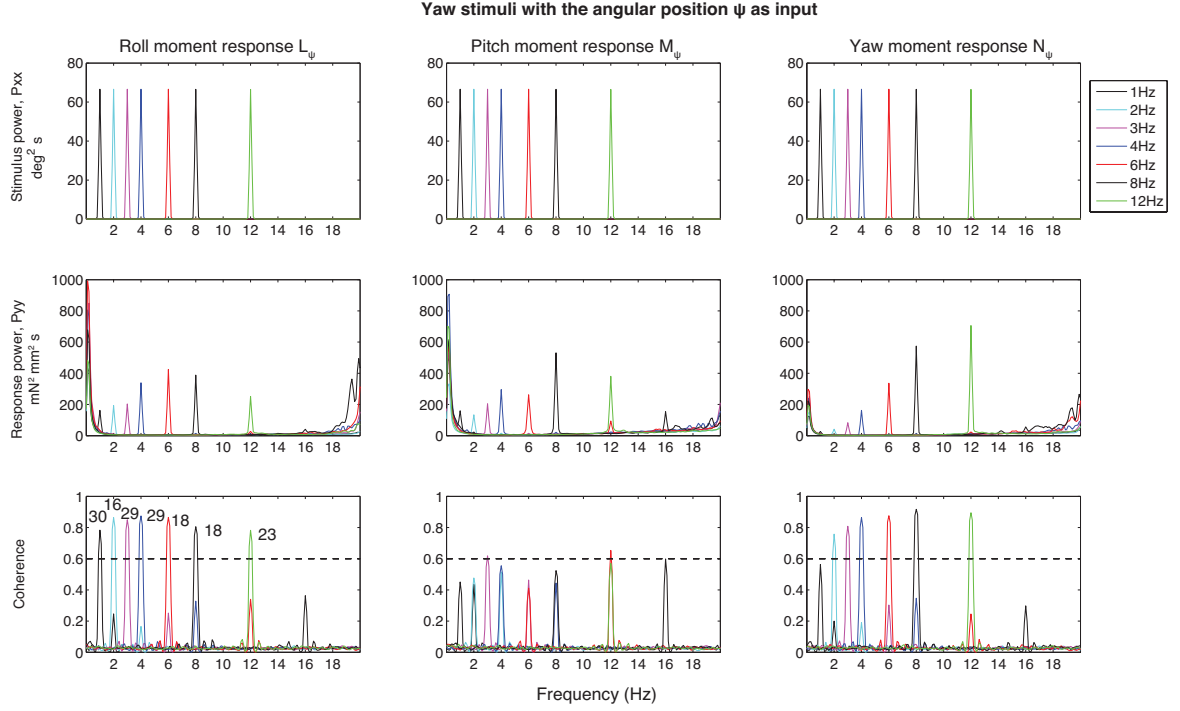


**Figure B.3:** Frequency spectra for seven single-sine yaw oscillations of  $5^\circ$  amplitude, ranging from 1 Hz to 12 Hz. The top row show the power spectrum of the stimulus. The second row shows the power spectrum of the response. The third row shoe the coherence, i.e. the amount of power of the stimulus that is linearly transferred to the response. Each colour relates to one individual stimulus. The responses are plotted across a frequency spectrum of 0 to 20 Hz on a linear scale. The numbers in the coherence plot indicate the number of trials averaged for that specific stimulus. Below the wingbeat frequency at  $\sim 23$  Hz, the bulk response power is provided at the fundamental oscillation frequency.

Appendix B Appendix chapter 3

**Table B.1:** AICc analysis for 16 competing models fitted to the magnitude of the roll moment responses to roll stimuli.

| variable | model                     | n   | k  | SSE | AICc | Lh   |
|----------|---------------------------|-----|----|-----|------|------|
| $L_\phi$ | $A + f^2$                 | 242 | 41 | 43  | -320 | 0.07 |
| $L_\phi$ | $A + Af + f^2$            | 242 | 42 | 42  | -320 | 0.06 |
| $L_\phi$ | $Af + f^2$                | 242 | 41 | 42  | -322 | 0.25 |
| $L_\phi$ | $A + f + Af + Af^2$       | 242 | 43 | 42  | -317 | 0.02 |
| $L_\phi$ | $A + f + Af^2$            | 242 | 42 | 43  | -319 | 0.04 |
| $L_\phi$ | $f^2$                     | 242 | 40 | 45  | -312 | 0.00 |
| $L_\phi$ | $A + f + f^2$             | 242 | 42 | 43  | -317 | 0.02 |
| $L_\phi$ | $A + f + Af + f^2 + Af^2$ | 242 | 44 | 42  | -318 | 0.03 |
| $L_\phi$ | $A + f + Af + f^2$        | 242 | 43 | 42  | -317 | 0.02 |
| $L_\phi$ | $Af$                      | 242 | 40 | 42  | -325 | 1.00 |
| $L_\phi$ | $A$                       | 242 | 40 | 45  | -311 | 0.00 |
| $L_\phi$ | $f$                       | 242 | 40 | 45  | -311 | 0.00 |
| $L_\phi$ | $f + Af$                  | 242 | 41 | 42  | -323 | 0.29 |
| $L_\phi$ | $A + Af$                  | 242 | 41 | 42  | -323 | 0.27 |
| $L_\phi$ | $A + f$                   | 242 | 41 | 43  | -319 | 0.05 |
| $L_\phi$ | $A + f + Af$              | 242 | 42 | 42  | -320 | 0.07 |

**Table B.2:** AICc analysis for 16 competing models fitted to the magnitude of the pitch moment responses to pitch stimuli.

| variable   | model                     | n   | k  | SSE | AICc | Lh   |
|------------|---------------------------|-----|----|-----|------|------|
| $M_\theta$ | $A + f^2$                 | 222 | 36 | 126 | -39  | 0.00 |
| $M_\theta$ | $A + Af + f^2$            | 222 | 37 | 124 | -40  | 0.00 |
| $M_\theta$ | $Af + f^2$                | 222 | 36 | 130 | -33  | 0.00 |
| $M_\theta$ | $A + f + Af + Af^2$       | 222 | 38 | 118 | -49  | 0.01 |
| $M_\theta$ | $A + f + Af^2$            | 222 | 37 | 122 | -43  | 0.00 |
| $M_\theta$ | $f^2$                     | 222 | 35 | 132 | -32  | 0.00 |
| $M_\theta$ | $A + f + f^2$             | 222 | 37 | 115 | -57  | 1.00 |
| $M_\theta$ | $A + f + Af + f^2 + Af^2$ | 222 | 39 | 113 | -54  | 0.20 |
| $M_\theta$ | $A + f + Af + f^2$        | 222 | 38 | 115 | -54  | 0.25 |
| $M_\theta$ | $Af$                      | 222 | 35 | 134 | -28  | 0.00 |
| $M_\theta$ | $A$                       | 222 | 35 | 130 | -35  | 0.00 |
| $M_\theta$ | $f$                       | 222 | 35 | 128 | -38  | 0.00 |
| $M_\theta$ | $f + Af$                  | 222 | 36 | 125 | -41  | 0.00 |
| $M_\theta$ | $A + Af$                  | 222 | 36 | 125 | -41  | 0.00 |
| $M_\theta$ | $A + f$                   | 222 | 36 | 124 | -43  | 0.00 |
| $M_\theta$ | $A + f + Af$              | 222 | 37 | 124 | -40  | 0.00 |

**Table B.3:** AICc analysis for 16 competing models fitted to the magnitude of the yaw and roll moment responses to yaw stimuli.

| variable | model                     | n   | k  | SSE | AICc | Lh   |
|----------|---------------------------|-----|----|-----|------|------|
| $N_\psi$ | $A + f^2$                 | 190 | 36 | 63  | -120 | 0.00 |
| $N_\psi$ | $A + Af + f^2$            | 190 | 37 | 58  | -133 | 0.00 |
| $N_\psi$ | $Af + f^2$                | 190 | 36 | 59  | -133 | 0.00 |
| $N_\psi$ | $A + f + Af + Af^2$       | 190 | 38 | 31  | -250 | 0.26 |
| $N_\psi$ | $A + f + Af^2$            | 190 | 37 | 31  | -253 | 1.00 |
| $N_\psi$ | $f^2$                     | 190 | 35 | 92  | -52  | 0.00 |
| $N_\psi$ | $Af$                      | 190 | 35 | 134 | 20   | 0.00 |
| $N_\psi$ | $A + f + f^2$             | 190 | 37 | 52  | -154 | 0.00 |
| $N_\psi$ | $A + f + Af + f^2 + Af^2$ | 190 | 39 | 31  | -247 | 0.06 |
| $N_\psi$ | $A + f + Af + f^2$        | 190 | 38 | 31  | -249 | 0.15 |
| $N_\psi$ | $A$                       | 190 | 35 | 104 | -28  | 0.00 |
| $N_\psi$ | $f$                       | 190 | 35 | 82  | -74  | 0.00 |
| $N_\psi$ | $f + Af$                  | 190 | 36 | 37  | -220 | 0.00 |
| $N_\psi$ | $A + Af$                  | 190 | 36 | 83  | -67  | 0.00 |
| $N_\psi$ | $A + f$                   | 190 | 36 | 55  | -146 | 0.00 |
| $N_\psi$ | $A + f + Af$              | 190 | 37 | 35  | -226 | 0.00 |
| $L_\psi$ | $A + f + Af + Af^2$       | 190 | 38 | 39  | -206 | 0.01 |
| $L_\psi$ | $A + f + Af^2$            | 190 | 37 | 41  | -197 | 0.00 |
| $L_\psi$ | $f^2$                     | 190 | 35 | 67  | -113 | 0.00 |
| $L_\psi$ | $A + Af + f^2$            | 190 | 37 | 47  | -172 | 0.00 |
| $L_\psi$ | $A + f^2$                 | 190 | 36 | 47  | -175 | 0.00 |
| $L_\psi$ | $Af + f^2$                | 190 | 36 | 53  | -152 | 0.00 |
| $L_\psi$ | $A + f + f^2$             | 190 | 37 | 39  | -207 | 0.01 |
| $L_\psi$ | $Af$                      | 190 | 35 | 59  | -136 | 0.00 |
| $L_\psi$ | $A + f + Af + f^2 + Af^2$ | 190 | 39 | 37  | -214 | 0.44 |
| $L_\psi$ | $A + f + Af + f^2$        | 190 | 38 | 37  | -215 | 1.00 |
| $L_\psi$ | $A$                       | 190 | 35 | 47  | -178 | 0.00 |
| $L_\psi$ | $f$                       | 190 | 35 | 67  | -113 | 0.00 |
| $L_\psi$ | $f + Af$                  | 190 | 36 | 46  | -178 | 0.00 |
| $L_\psi$ | $A + Af$                  | 190 | 36 | 47  | -175 | 0.00 |
| $L_\psi$ | $A + f$                   | 190 | 36 | 47  | -175 | 0.00 |
| $L_\psi$ | $A + f + Af$              | 190 | 37 | 45  | -179 | 0.00 |

Appendix B Appendix chapter 3

**Table B.4:** AICc analysis for 16 competing models fitted to the phase of the roll moment responses to roll stimuli.

| variable | model                     | n   | k  | SSE    | AICc | Lh   |
|----------|---------------------------|-----|----|--------|------|------|
| $L_\phi$ | $A + f^2$                 | 242 | 41 | 132448 | 1625 | 0.00 |
| $L_\phi$ | $A + Af + f^2$            | 242 | 42 | 130610 | 1625 | 0.00 |
| $L_\phi$ | $A + f + Af + Af^2$       | 242 | 43 | 89770  | 1537 | 0.23 |
| $L_\phi$ | $A + f + Af^2$            | 242 | 42 | 93884  | 1545 | 0.00 |
| $L_\phi$ | $f^2$                     | 242 | 40 | 145069 | 1644 | 0.00 |
| $L_\phi$ | $Af$                      | 242 | 40 | 338852 | 1849 | 0.00 |
| $L_\phi$ | $A + f + Af + f^2 + Af^2$ | 242 | 44 | 89733  | 1540 | 0.05 |
| $L_\phi$ | $Af + f^2$                | 242 | 41 | 131253 | 1623 | 0.00 |
| $L_\phi$ | $A + f + f^2$             | 242 | 42 | 107603 | 1578 | 0.00 |
| $L_\phi$ | $A + f + Af + f^2$        | 242 | 43 | 89773  | 1537 | 0.23 |
| $L_\phi$ | $A$                       | 242 | 40 | 448548 | 1917 | 0.00 |
| $L_\phi$ | $f$                       | 242 | 40 | 119815 | 1598 | 0.00 |
| $L_\phi$ | $f + Af$                  | 242 | 41 | 93555  | 1541 | 0.03 |
| $L_\phi$ | $A + Af$                  | 242 | 41 | 217211 | 1745 | 0.00 |
| $L_\phi$ | $A + f$                   | 242 | 41 | 107650 | 1575 | 0.00 |
| $L_\phi$ | $A + f + Af$              | 242 | 42 | 89773  | 1534 | 1.00 |

**Table B.5:** AICc analysis for 16 competing models fitted to the phase of the pitch moment responses to pitch stimuli.

| variable   | model                     | n   | k  | SSE    | AICc | Lh   |
|------------|---------------------------|-----|----|--------|------|------|
| $M_\theta$ | $A + f^2$                 | 222 | 36 | 125763 | 1494 | 0.01 |
| $M_\theta$ | $A + Af + f^2$            | 222 | 37 | 119169 | 1485 | 1.00 |
| $M_\theta$ | $A + f + Af + Af^2$       | 222 | 38 | 125582 | 1499 | 0.00 |
| $M_\theta$ | $A + f + Af^2$            | 222 | 37 | 137908 | 1517 | 0.00 |
| $M_\theta$ | $f^2$                     | 222 | 35 | 168688 | 1556 | 0.00 |
| $M_\theta$ | $Af$                      | 222 | 35 | 365187 | 1728 | 0.00 |
| $M_\theta$ | $A + f + Af + f^2 + Af^2$ | 222 | 39 | 124990 | 1501 | 0.00 |
| $M_\theta$ | $Af + f^2$                | 222 | 36 | 140951 | 1519 | 0.00 |
| $M_\theta$ | $A + f + f^2$             | 222 | 37 | 144740 | 1528 | 0.00 |
| $M_\theta$ | $A + f + Af + f^2$        | 222 | 38 | 125055 | 1498 | 0.00 |
| $M_\theta$ | $A$                       | 222 | 35 | 386145 | 1740 | 0.00 |
| $M_\theta$ | $f$                       | 222 | 35 | 167941 | 1555 | 0.00 |
| $M_\theta$ | $f + Af$                  | 222 | 36 | 131213 | 1503 | 0.00 |
| $M_\theta$ | $A + Af$                  | 222 | 36 | 240288 | 1637 | 0.00 |
| $M_\theta$ | $A + f$                   | 222 | 36 | 148344 | 1530 | 0.00 |
| $M_\theta$ | $A + f + Af$              | 222 | 37 | 127575 | 1500 | 0.00 |

**Table B.6:** AICc analysis for 16 competing models fitted to the phase of the yaw and roll moment responses to yaw stimuli.

| variable | model                     | n   | k  | SSE     | AICc | Lh   |
|----------|---------------------------|-----|----|---------|------|------|
| $N_\psi$ | $A + f^2$                 | 190 | 36 | 114656  | 1306 | 0.00 |
| $N_\psi$ | $A + Af + f^2$            | 190 | 37 | 114176  | 1308 | 0.00 |
| $N_\psi$ | $A + f + Af + Af^2$       | 190 | 38 | 96891   | 1280 | 0.06 |
| $N_\psi$ | $A + f + Af^2$            | 190 | 37 | 111205  | 1303 | 0.00 |
| $N_\psi$ | $f^2$                     | 190 | 35 | 121165  | 1313 | 0.00 |
| $N_\psi$ | $Af$                      | 190 | 35 | 625311  | 1625 | 0.00 |
| $N_\psi$ | $A + f + Af + f^2 + Af^2$ | 190 | 39 | 93116   | 1276 | 0.53 |
| $N_\psi$ | $Af + f^2$                | 190 | 36 | 114881  | 1306 | 0.00 |
| $N_\psi$ | $A + f + f^2$             | 190 | 37 | 102206  | 1287 | 0.00 |
| $N_\psi$ | $A + f + Af + f^2$        | 190 | 38 | 94057   | 1275 | 1.00 |
| $N_\psi$ | $A$                       | 190 | 35 | 983384  | 1711 | 0.00 |
| $N_\psi$ | $f$                       | 190 | 35 | 116312  | 1306 | 0.00 |
| $N_\psi$ | $f + Af$                  | 190 | 36 | 107144  | 1293 | 0.00 |
| $N_\psi$ | $A + Af$                  | 190 | 36 | 327804  | 1506 | 0.00 |
| $N_\psi$ | $A + f$                   | 190 | 36 | 113285  | 1304 | 0.00 |
| $N_\psi$ | $A + f + Af$              | 190 | 37 | 103702  | 1290 | 0.00 |
| $L_\psi$ | $A + f^2$                 | 190 | 36 | 192306  | 1404 | 0.00 |
| $L_\psi$ | $A + Af + f^2$            | 190 | 37 | 187355  | 1402 | 0.00 |
| $L_\psi$ | $A + f + Af + Af^2$       | 190 | 38 | 135126  | 1343 | 1.00 |
| $L_\psi$ | $A + f + Af^2$            | 190 | 37 | 153122  | 1364 | 0.00 |
| $L_\psi$ | $f^2$                     | 190 | 35 | 199054  | 1408 | 0.00 |
| $L_\psi$ | $Af$                      | 190 | 35 | 755869  | 1661 | 0.00 |
| $L_\psi$ | $A + f + Af + f^2 + Af^2$ | 190 | 39 | 135117  | 1347 | 0.21 |
| $L_\psi$ | $Af + f^2$                | 190 | 36 | 187524  | 1399 | 0.00 |
| $L_\psi$ | $A + f + f^2$             | 190 | 37 | 166278  | 1380 | 0.00 |
| $L_\psi$ | $A + f + Af + f^2$        | 190 | 38 | 135539  | 1344 | 0.75 |
| $L_\psi$ | $A$                       | 190 | 35 | 1113297 | 1735 | 0.00 |
| $L_\psi$ | $f$                       | 190 | 35 | 173313  | 1381 | 0.00 |
| $L_\psi$ | $f + Af$                  | 190 | 36 | 154900  | 1363 | 0.00 |
| $L_\psi$ | $A + Af$                  | 190 | 36 | 455659  | 1568 | 0.00 |
| $L_\psi$ | $A + f$                   | 190 | 36 | 170268  | 1381 | 0.00 |
| $L_\psi$ | $A + f + Af$              | 190 | 37 | 138026  | 1344 | 0.64 |

# Appendix C

## Appendix chapter 4

### C.1 Power spectra and coherence for single-sine stimuli

$p'$ ,  $r'$ , and  $p''$

### C.2 Statistics for the 95% confidence intervals

*lscov* returns the ordinary least squares solution for the linear system but it does not give any confidence intervals or goodness of fit. To obtain the confidence intervals we apply the Cholesky transform to the diagonal matrix of variances which gives us the triangular matrix  $P=\text{chol}(\text{diag}(\text{variances}))$ . With  $P$  we then transform the measured responses  $Y$  into  $Z=P \backslash Y$  and the predictors  $x$  into  $U=P \backslash x$  [83]. We then apply the linear regression  $\text{regress}(Z,U)$  and obtain the model parameters  $B$  (which are equivalent to those given by the function *lscov*, i.e. they remain unaffected by the Cholesky transformation) and the corresponding confidence intervals and the R squared value of the model. Basically, the transformation is performed in order to use a general least squares function rather the

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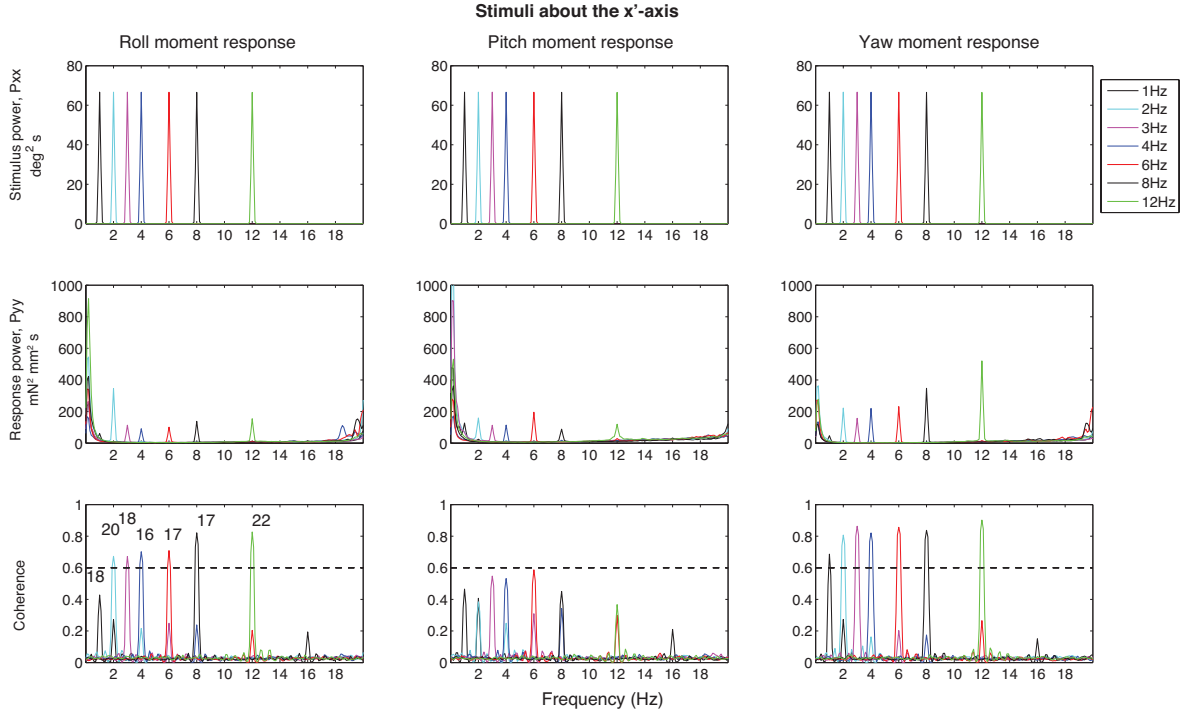


**Figure C.1:** Power spectra for oscillations about the longitudinal axis  $x'$ . The top row shows the stimulus power. The second row shows that the response power is generated at the frequency of the stimulus without harmonic content. The third row shows the coherence. The numbers indicate the number of trials averaged to evaluate the total mean response power and coherence. The columns show the spectra for the moment responses about the x-, y-, and z-axis.

the ordinary least squares function.

### C.3 Goodness of fit for linear models without intercept

$R_u^2$  in equation C.1 is the uncentered  $R^2$  for a model without intercept [84]. In a model with intercept, the goodness of fit refers to the amount of variance explained around the mean of the data. Hence, the total sum of squares in the denominator contains the mean value  $\bar{y}$ . The model usually accounts for non-zero means with the intercept. In this study,

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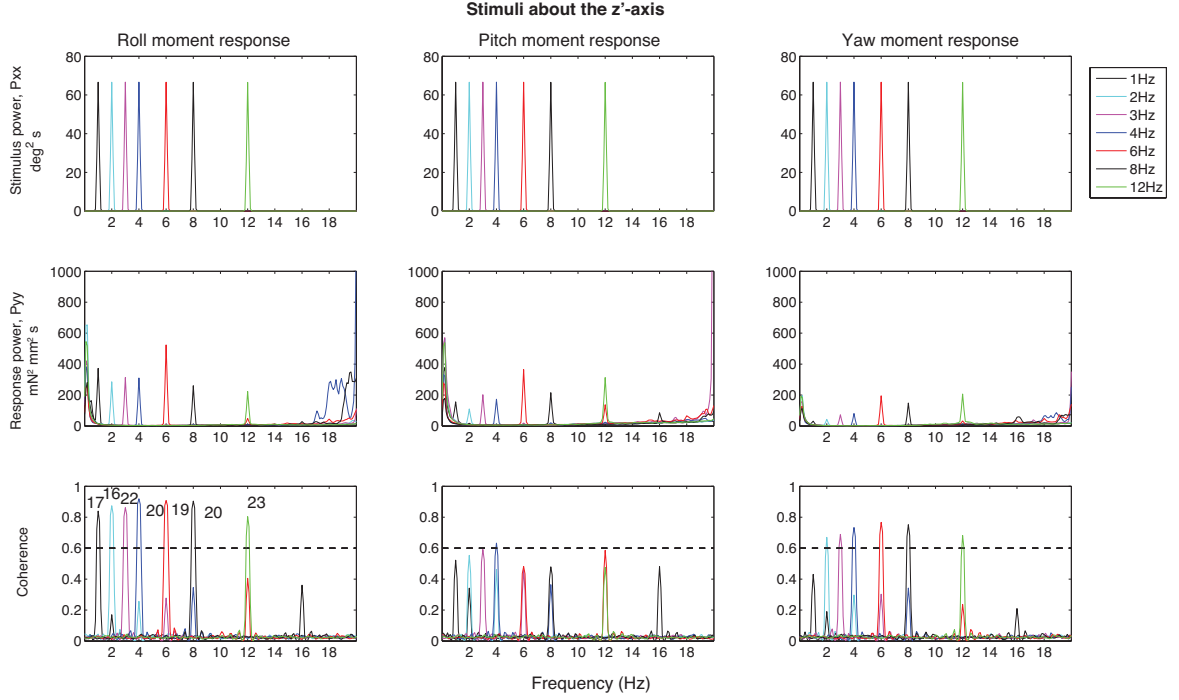


**Figure C.2:** Power spectra for oscillations about the dorso-ventral axis  $z'$ . The top row shows the stimulus power. The second row shows that the response power is generated at the frequency of the stimulus without harmonic content. The third row shows the coherence. The numbers indicate the number of trials averaged to evaluate the total mean response power and coherence. The columns show the spectra for the moment responses about the x-, y-, and z-axis.

the response to a zero-state input will be zero. Hence, the model is forced through the origin and no intercept is accounted for in our model fitting. Note that the denominator for  $R_u^2$  is larger than for  $R^2$  and therefore delivers higher values for the goodness of fit.

$$R_u^2 = 1 - \frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{\sum_{i=1}^n y_i^2} \quad (\text{C.1})$$

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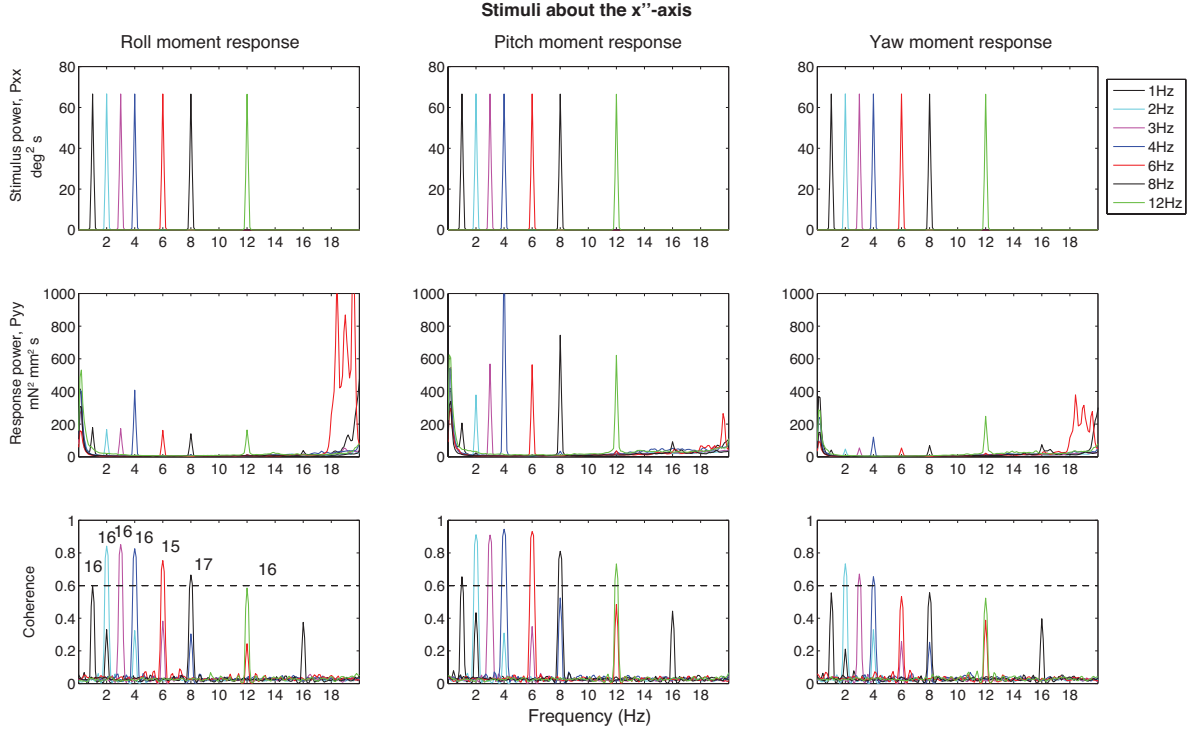


**Figure C.3:** Power spectra for oscillations about the axis  $x''$ . The top row shows the stimulus power. The second row shows that the response power is generated at the frequency of the stimulus without harmonic content. The third row shows the coherence. The numbers indicate the number of trials averaged to evaluate the total mean response power and coherence. The columns show the spectra for the sensor axes  $x$ ,  $y$ , and  $z$ .

### C.4 Fitting PID-controllers to individual roll and yaw moments generated in response to lateral stimuli

I fitted a PID model with a time delay to the 14 data points of each moment response  $L$  and  $N$  for stimuli  $p$ ,  $r$ ,  $p'$  and  $r'$ . The mean square error is minimised separately for  $L$  and  $N$ . The results are presented in tables C.1 and C.2 and plotted in figure C.4.

**Table C.1:** Fitting PID models with individual time delays to the roll moment responses  $L$  for stimuli  $p$ ,  $r$ ,  $p'$  and  $r'$ .

|         | $L_p$   | $L_r$  | $L_{p'}$ | $L_{r'}$ |
|---------|---------|--------|----------|----------|
| k       | 5       | 5      | 5        | 5        |
| n       | 14      | 14     | 14       | 14       |
| $R_u^2$ | 0.98    | 0.67   | 0.17     | 0.91     |
| $\tau$  | 0.007   | 0.074  | 0.045    | 0.000    |
| $K_P$   | -0.0125 | 0.0320 | 0.0148   | -0.0144  |
| $K_I$   | 1.4181  | 0.1999 | -0.2976  | 1.6100   |
| $K_D$   | 0.0003  | 0.0000 | 0.0000   | 0.0005   |

**Table C.2:** Fitting separate PID models with individual time delays to yaw moment responses  $N$  for stimuli  $p$ ,  $r$ ,  $p'$  and  $r'$ .

|         | $N_p$   | $N_r$  | $N_{p'}$ | $N_{r'}$ |
|---------|---------|--------|----------|----------|
| k       | 5       | 5      | 5        | 5        |
| n       | 14      | 14     | 14       | 14       |
| $R_u^2$ | 0.61    | 0.86   | 0.69     | 0.65     |
| $\tau$  | 0.088   | 0.057  | 0.061    | 0.053    |
| $K_P$   | -0.0059 | 0.0379 | -0.0340  | 0.0191   |
| $K_I$   | -0.4778 | 0.0030 | -0.0370  | -0.3350  |
| $K_D$   | -0.0002 | 0.0000 | 0.0000   | 0.0000   |

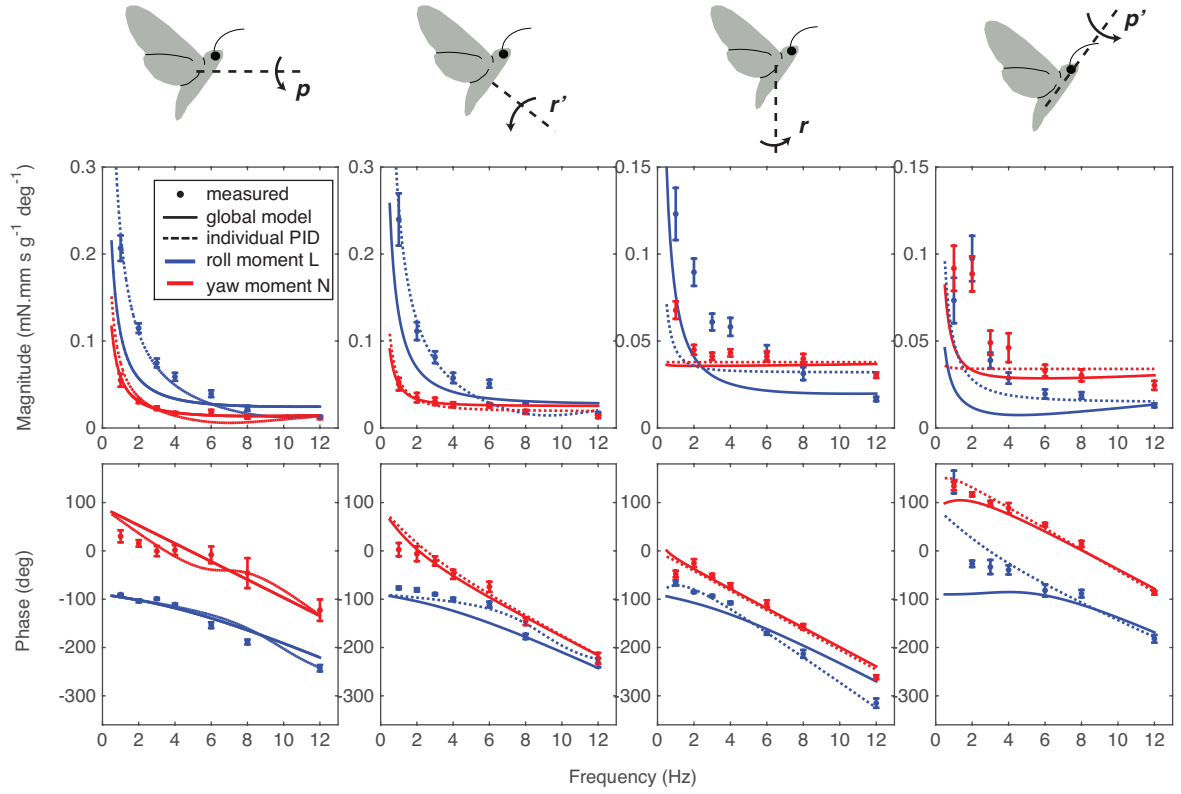


**Figure C.4:** A PID-controller with an individual time delay is fitted to the seven mean responses of each stimulus moment (dashed). The colours indicate the roll moment (blue) and the yaw moment (red) responses. The measured data is indicated with the standard error of the mean. The individual models are compared to the best fitting general model (full line).