A fly-robot interface to investigate the dynamics of closed-loop visuo-motor control in the blowfly

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Declaration

I herewith certify that all material in this dissertation is my own work except for the fly preparation and electrophysiology which was performed by Drs Kris D. Peterson and Kit C. Longden, while I was responsible for the operation of the closed-loop systems and the control of the stimulation regimes.

Naveed Ejaz
Abstract

The blowfly Calliphora is one of the most sophisticated fliers in the animal kingdom. It displays a broad repertoire of visually guided behaviours that can readily be quantified, including gaze and flight stabilization reflexes, male chasing flights, collision avoidance and landing responses. The fly achieves such robust visuomotor control tasks based on a comparatively simple nervous system that is highly accessible for electrophysiological recordings. The ability to investigate the fly’s performance at the behavioural and electrophysiology levels makes this animal an ideal model system to study closed-loop visual motor control.

The aim of this thesis was to develop and characterize the dynamics of a fly-robot interface (FRI) while a fly performs a closed-loop visual stabilization task.

A novel experimental setup involving a FRI was developed which allowed for simultaneous measurements of neural activity from the fly and the behavioural performance of the robot. In the setup, the neural activity of an identified visual interneuron, the H1 cell, was recorded and its action potentials were used to control the motion of a mobile robot that was free to rotate along its vertical axis. External visual perturbations were introduced into the closed-loop system through a rotating turn-table with the robot using the neural activity to counter-rotate and to minimize the observed visual motion. The closed-loop control delay of the FRI was 50 ms which is well within the range of visual response delays observed in fly behaviour.

With the FRI, the closed-loop dynamics of a static-gain proportional controller were characterized. The results explain significant oscillations in the closed-loop responses as a possible consequence of a high controller gain which were also observed but never fully interpreted in previous behavioural studies. Varying the
controller gain also offers competing control benefits to the fly, with different gains maximizing performance for different input frequency ranges and thus different behavioural tasks.

Results with the proportional controller indicate the dependence of the FRI frequency response on the angular acceleration of visual motion. An adaptive controller designed to dynamically scale the feedback gain was found to increase the bandwidth of the frequency response when compared with the static-gain proportional controller.

The image velocities observed under closed-loop conditions using the proportional and the adaptive controllers were correlated with the spiking activity of the H1-cell. A remarkable qualitative similarity was found between the response dynamics of the cell under closed-loop conditions with those obtained in previous open-loop experiments. Specifically, (i) the peak spike rate decreased when the mean image velocity was increased, (ii) the relationship between spike rate and image velocity was dependent on the standard deviation of the image velocities suggesting adaptive scaling of the cell’s signalling range, and (iii) the cell’s gain decreased linearly with increasing image accelerations.

Despite the fact that several sensory modalities - including the motion vision pathway - process information in a non-linear fashion signal integration at stages one to two synapses away from the motor systems and the behavioural output itself have been shown to be linear. Quantifying the closed-loop dynamics of visuo-motor control at both the behavioural and neuronal level, may provide a starting point to discover the neural mechanisms underlying an appropriate combination of complementary non-linear processes which ultimately result in a linear performance of the overall system.
To my supervisor Holger - I would like to thank you for your tireless supervision and support. You stuck with me even during times of personal crisis and I truly could not have completed this work without your patience, support and mentorship.

Kit - thank you for being a surrogate supervisor and a great friend. For helping me run numerous experiments, to training me in the techniques and just answering my inane questions, thank you.

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Finally, none of this would have been possible without the unconditional support of my parents and my sisters. I owe them more than I can list down.
In memory of Lila Rashid and the three boys from Dugout
3. Dynamics of closed-loop visuo-motor stabilization under proportional control

3.1. Closing the loop for the fly-robot interface
   3.1.1. Fly-robot interface for optomotor control
   3.1.2. Proportional controller as a static gain feedback controller
   3.1.3. Closed-loop proportional control
   3.1.4. Closed-loop Experiments

3.2. Step Response Characterization

3.3. Frequency Response Characterization
   3.3.1. Performance Index

3.4. Discussion

4. Adaptive gain control strategy for visuo-motor stabilization

4.1. Adaptive gain control
   4.1.1. Description of the adaptive controller
   4.1.2. Closed-loop experiments

4.2. Frequency response characterization
   4.2.1. Sample responses
   4.2.2. Bode magnitude and phase plots

4.3. Step Response Characterization

4.4. Discussion

5. Neural responses under closed-loop conditions

5.1. Adaptive re-scaling properties of the H1-cell

5.2. Experimental Methods

5.3. Adaptive re-scaling in closed-loop
   5.3.1. Effect of the moments of the stimulus velocity distribution on the H1 response function

5.4. Closed-loop H1 frequency response function

5.5. Discussion
6. Concluding Remarks

6.1. Summary ......................................................... 135

6.1.1. Key Contributions .......................................... 138

6.2. General Discussion ........................................... 139

6.2.1. Reductionist approach to studying neural strategies for visuo-
        motor control .............................................. 139

6.2.2. Robustness of the optomotor response ...................... 140

6.2.3. Choice of the robot controller for providing real-world dy-
        namics ...................................................... 140

6.2.4. Choice of methods for characterizing neural and FRI dy-
        namics ...................................................... 141

6.2.5. Linear versus nonlinear control ............................ 142

6.2.6. Natural frequency of the FRI system ......................... 144

6.3. Future work ...................................................... 145

Appendices

A. Appendix .......................................................... 150

A.1. Optic Flow ...................................................... 150

A.2. Derivation for F → E ............................................ 155

B. Publications and Conference Proceedings ...................... 160

Bibliography .......................................................... 162
# List of Figures

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.1</td>
<td>Self-motion and the major sensory systems of the blowfly</td>
<td>19</td>
</tr>
<tr>
<td>1.2</td>
<td>Contributions of different sensory systems to compensatory head roll responses in <em>Calliphora</em></td>
<td>26</td>
</tr>
<tr>
<td>1.3</td>
<td>Anatomical organization of the visual system of the blowfly</td>
<td>27</td>
</tr>
<tr>
<td>1.4</td>
<td>LPTCs as matched filters for optic flow</td>
<td>28</td>
</tr>
<tr>
<td>1.5</td>
<td>Processing local direction of motion with EMDs</td>
<td>29</td>
</tr>
<tr>
<td>1.6</td>
<td>H1 and HSE receptive fields and connectivity</td>
<td>30</td>
</tr>
<tr>
<td>1.7</td>
<td>Components of the fly optomotor response</td>
<td>31</td>
</tr>
<tr>
<td>2.1</td>
<td>Experimental design for the closed-loop visual stabilization task with the FRI</td>
<td>43</td>
</tr>
<tr>
<td>2.2</td>
<td>ASURO Robot before and after custom modifications</td>
<td>45</td>
</tr>
<tr>
<td>2.3</td>
<td>Relationship between $V_r$ and $\omega_r$</td>
<td>47</td>
</tr>
<tr>
<td>2.4</td>
<td>Frequency response characterization of the robot rotation</td>
<td>48</td>
</tr>
<tr>
<td>2.5</td>
<td>Relationship between $V_p$ and $\omega_p$</td>
<td>50</td>
</tr>
<tr>
<td>2.6</td>
<td>Relationship between $V_p$ and $\omega_p$</td>
<td>51</td>
</tr>
<tr>
<td>2.7</td>
<td>Frequency response characterization of the turn-table rotation</td>
<td>52</td>
</tr>
<tr>
<td>2.8</td>
<td>CRT monitor placement and electromagnetic shielding</td>
<td>53</td>
</tr>
<tr>
<td>2.9</td>
<td>Dendritic arbourization and response field of the H1 cell</td>
<td>55</td>
</tr>
<tr>
<td>2.10</td>
<td>Block diagram for closed-loop control</td>
<td>56</td>
</tr>
<tr>
<td>2.11</td>
<td>Software interface for closed-loop control</td>
<td>58</td>
</tr>
<tr>
<td>2.12</td>
<td>Electrophysiology recording of an H1 cell</td>
<td>59</td>
</tr>
<tr>
<td>2.13</td>
<td>Frequency drop-off using different spike rate estimation kernels</td>
<td>60</td>
</tr>
<tr>
<td>2.14</td>
<td>Systems identification using a step input</td>
<td>63</td>
</tr>
<tr>
<td>Section</td>
<td>Page</td>
<td></td>
</tr>
<tr>
<td>------------------------------------------------------------------------</td>
<td>------</td>
<td></td>
</tr>
<tr>
<td>2.15. Calibration of LK method</td>
<td>67</td>
<td></td>
</tr>
<tr>
<td>2.16. Optic flow characterization statistics</td>
<td>68</td>
<td></td>
</tr>
<tr>
<td>3.1. Optomotor control using the FRI</td>
<td>72</td>
<td></td>
</tr>
<tr>
<td>3.2. Block diagram of a generic PID controller</td>
<td>72</td>
<td></td>
</tr>
<tr>
<td>3.3. Block diagram of closed-loop FRI using a proportional controller.</td>
<td>74</td>
<td></td>
</tr>
<tr>
<td>3.4. $F_{\text{max}}$ estimates for the H1 cell</td>
<td>75</td>
<td></td>
</tr>
<tr>
<td>3.5. Sigmoid function used to map $F$ to $E$ for motion in the PD and ND</td>
<td>76</td>
<td></td>
</tr>
<tr>
<td>3.6. Mean step response of the FRI with the proportional controller</td>
<td>77</td>
<td></td>
</tr>
<tr>
<td>3.7. Step response characterization for the proportional controller</td>
<td>78</td>
<td></td>
</tr>
<tr>
<td>3.8. Sample turn-table vs robot responses for sinusoidal inputs</td>
<td>81</td>
<td></td>
</tr>
<tr>
<td>3.9. Bode system gain and phase plots for the FRI with a proportional controller</td>
<td>82</td>
<td></td>
</tr>
<tr>
<td>3.10. Performance Index for the proportional controller with sinusoidal inputs</td>
<td>84</td>
<td></td>
</tr>
<tr>
<td>4.1. Optimal stimulus response function for a single input single output neuron</td>
<td>94</td>
<td></td>
</tr>
<tr>
<td>4.2. Comparative block diagrams of the closed-loop FRI using the adaptive and proportional controllers</td>
<td>95</td>
<td></td>
</tr>
<tr>
<td>4.3. Re-scaling of the spiking rate mapped onto the compensation error for the adaptive controller</td>
<td>96</td>
<td></td>
</tr>
<tr>
<td>4.4. Examples of turntable versus robot responses upon sinusoidal inputs for the adaptive controller</td>
<td>99</td>
<td></td>
</tr>
<tr>
<td>4.5. Comparison of turntable versus robot responses upon sinusoidal inputs for the adaptive and the proportional controllers</td>
<td>100</td>
<td></td>
</tr>
<tr>
<td>4.6. Bode magnitude and phase plots for the adaptive and proportional controllers</td>
<td>103</td>
<td></td>
</tr>
<tr>
<td>4.7. DC system gain and bandwidth for an ideal low-pass filter</td>
<td>104</td>
<td></td>
</tr>
<tr>
<td>4.8. Bandwidth and DC-gain of the adaptive and the proportional controllers</td>
<td>105</td>
<td></td>
</tr>
<tr>
<td>4.9. Proposed performance indexes for the adaptive and proportional controllers</td>
<td>106</td>
<td></td>
</tr>
<tr>
<td>Section</td>
<td>Title</td>
<td></td>
</tr>
<tr>
<td>---------</td>
<td>-------</td>
<td></td>
</tr>
<tr>
<td>4.10.</td>
<td>Mean step response of the fly-robot interface for the adaptive controller</td>
<td></td>
</tr>
<tr>
<td>4.11.</td>
<td>Comparison of step response performance of adaptive and proportional controllers</td>
<td></td>
</tr>
<tr>
<td>5.1.</td>
<td>Response of the H1-cell to motion of a visual grating along its preferred and null direction</td>
<td></td>
</tr>
<tr>
<td>5.2.</td>
<td>Adaptive re-scaling property of the H1-cell</td>
<td></td>
</tr>
<tr>
<td>5.3.</td>
<td>Relationship between slip-speed and spiking rate under closed-loop conditions</td>
<td></td>
</tr>
<tr>
<td>5.4.</td>
<td>Mean, standard deviation and peak velocity of the slip-speed distributions with the proportional controller</td>
<td></td>
</tr>
<tr>
<td>5.5.</td>
<td>Sigmoid fitting of the slip-speed vs spiking rate response function for the step response of the FRI under proportional control</td>
<td></td>
</tr>
<tr>
<td>5.6.</td>
<td>Sigmoid fitting of the normalized slip-speed vs spiking rate response function for the step response of the FRI under proportional control</td>
<td></td>
</tr>
<tr>
<td>5.7.</td>
<td>H1 frequency response function</td>
<td></td>
</tr>
<tr>
<td>5.8.</td>
<td>Statistics of the slip-speed distributions and H1 spiking rate in closed-loop</td>
<td></td>
</tr>
<tr>
<td>5.9.</td>
<td>The gain at each of the input frequencies ( f_i ) for the adaptive controller</td>
<td></td>
</tr>
<tr>
<td>5.10.</td>
<td>Effect of ( \sigma_v ) on the acceleration sensitivity of H1</td>
<td></td>
</tr>
<tr>
<td>6.1.</td>
<td>Micro-recording probe</td>
<td></td>
</tr>
<tr>
<td>A.1.</td>
<td>Solution space for the brightness constancy equation</td>
<td></td>
</tr>
<tr>
<td>A.2.</td>
<td>Aperture problem for estimating local motion</td>
<td></td>
</tr>
<tr>
<td>A.3.</td>
<td>F2E CB nonlinearity implemented as a cosine domain-range mapping</td>
<td></td>
</tr>
<tr>
<td>A.4.</td>
<td>Nonlinearities used in estimating F2E when ( F &gt; F_{spont} ) &amp; ( F &lt; F_{spont} )</td>
<td></td>
</tr>
</tbody>
</table>
List of Tables
# Acronyms & Nomenclature

<table>
<thead>
<tr>
<th>Acronym</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>LPTC</td>
<td>Lobula plate tangential cell</td>
</tr>
<tr>
<td>H1</td>
<td>Horizontally sensitive cell in the Lobula Plate</td>
</tr>
<tr>
<td>PD</td>
<td>Preferred direction of an LPTC</td>
</tr>
<tr>
<td>ND</td>
<td>Null or anti-preferred direction of an LPTC</td>
</tr>
<tr>
<td>FRI</td>
<td>Fly-robot interface</td>
</tr>
<tr>
<td>OF</td>
<td>Optic flow</td>
</tr>
<tr>
<td>CRT</td>
<td>Cathode ray tube</td>
</tr>
<tr>
<td>EMD</td>
<td>Elementary motion detector</td>
</tr>
<tr>
<td>SNR</td>
<td>Signal-to-noise</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\lambda_{sp}$</td>
<td>Pattern spatial wavelength</td>
</tr>
<tr>
<td>$F$</td>
<td>Instantaneous spiking rate</td>
</tr>
<tr>
<td>$F_s$</td>
<td>Spontaneous spiking rate</td>
</tr>
<tr>
<td>$F_{\text{max}}$</td>
<td>Maximum spiking rate</td>
</tr>
<tr>
<td>$E$</td>
<td>Compensation error</td>
</tr>
<tr>
<td>$f_i$</td>
<td>Turn-table input frequency</td>
</tr>
<tr>
<td>$\omega_p$</td>
<td>Turn-table angular velocity</td>
</tr>
<tr>
<td>$\omega_r$</td>
<td>Robot angular velocity</td>
</tr>
<tr>
<td>$V_r$</td>
<td>Robot input speed (8-bit number)</td>
</tr>
<tr>
<td>$K_p$</td>
<td>Static closed-loop gain for the proportional controller</td>
</tr>
<tr>
<td>$\Delta T_{ws}$</td>
<td>Window size over which adaptive controller estimates $F_{\text{max}}$</td>
</tr>
<tr>
<td>$G_{dc}$</td>
<td>DC gain</td>
</tr>
<tr>
<td>$f_c$</td>
<td>Cut-off frequency</td>
</tr>
<tr>
<td>$\mu_v$</td>
<td>Mean of the pattern velocity distribution</td>
</tr>
<tr>
<td>$\sigma_v$</td>
<td>Standard deviation of the pattern velocity distribution</td>
</tr>
</tbody>
</table>
1. Introduction

1.1. Motivation and Aims

Humans rely heavily on their vision for the control of movement. From seemingly basic tasks such as picking up an object to challenging tasks such as driving a car on a crowded road, our visual system is responsible for extracting information about the environment and providing the necessary feedback required for controlling our movements and achieving the desired task. The reliance on vision for the control of movement is observed across the animal kingdom. Millions of years of evolution have streamlined the neural processes that underlie the processing of visual input in order to control motion [Laughlin, 2001; Niven and Laughlin, 2008]. Currently, no man-made robotic controller can match the versatility or the dexterity of the human visuo-motor control system.

While reverse engineering voluntary visuo-motor control strategies and the underlying neural processes in humans seems to be an attractive prospect with obvious advantages, it is currently extremely hard to do due to technical and methodological challenges. Firstly, because of the highly invasive procedures involved, neural recordings in humans are currently only performed for patients with severe movement pathologies (e.g. epilepsy and Parkinson’s disease). Secondly, studying voluntary movement in humans at the neuronal level requires accounting for changes in visuo-motor performance due to the internal state of the subject (e.g. attention or level of fatigue). Attention, for example, has been shown to gate visual perception in both monkeys [Moran and Desimone, 1985] and humans [Li et al., 2002]. Visuo-motor control of voluntary motion is in contrast to involuntary vestibulo-
ocular (VOR) and the optokinetic (OKR) reflexes, both of which stabilize the position of the eye relative to the movement of the head [Kandel et al., 2000] and are unaffected by the internal state of the subject.

Voluntary and involuntary movements are examples of inner and outer-loop control strategies, respectively. Inner-loop control strategies are control loops with fast response times that are essential for the stabilization of gaze and posture in both vertebrates and invertebrates [Kandel et al., 2000, Krapp and Wicklein, 2008, Miles and Wallman, 1993]. Inner-loop controller’s work on the principle that the system to be controlled for has a desired equilibrium position or value that it will attempt to return to following an external perturbation. In contrast, an outer-loop controller can influence the equilibrium or set point of the inner-loop controller to achieve the desired behaviour. As a result, even though the position of the eye is under inner-loop control by both the VOR and OKR, the subject can still voluntarily move the position of his or her eyes to the desired position without a compensatory movement as a result of an inner-loop reflex.

The design of inner-loop controllers is usually much simpler than their outer-loop counterparts and can therefore be used to investigate visuo-motor control strategies and the underlying neuronal processes. Furthermore, inner-loop models of visuo-motor control can be studied in model systems that are as reliant on vision for behaviour as humans, yet have a neural system and architecture that are a few orders of magnitude less complex in terms of the number of neurons. The blowfly is one such model system that uses visuo-motor inner-loop control to stabilize its gaze [Krapp and Wicklein, 2008, Miles and Wallman, 1993]. It has a number of sensory systems but is highly reliant on its visual system for flight stability and gaze control. Finally, even though the blowfly has a rich array of behaviours (e.g. feeding, chasing) it achieves them with a relatively simple neural system that can be studied using electrophysiological techniques.

The aim of this thesis was to characterize the behavioural and neural dynamics observed while a fly performs a closed-loop visuo-motor task. In order to achieve this, a novel experimental setup consisting of a fly-robot interface (FRI) was developed that allowed for the simultaneous measurements of the neural activity and the behavioural performance with different closed-loop control strategies.
1.2. Outline of Thesis

A background of the fly visual system along with a literature review of studies involving inner-loop control principles that underlie visuo-motor control are presented in the remainder of this introductory chapter. The subsequent part of this thesis is structured into four main results chapters (Chapters 2-5).

In Chapter 2, a novel experimental system for investigating closed-loop visuo-motor control in the fly is described. The experimental system consists of a fly-robot interface (FRI) that was designed to simultaneously measure the neural activity from an identified visual interneuron as well as the fly’s behavioural performance within the FRI. The behavioural performance of the fly within the FRI was measured in terms of compensating for externally induced visual motion while the electrophysiological recordings of an identified visual interneuron (H1 cell) were used to provide the signals for closed-loop control.

In Chapter 3, a proportional controller with a static controller gain is described which was used to close the loop between the activity of the H1 cell and pattern motion within a visual stimulation arena. External visual perturbations with step and sinusoidal velocity profiles were introduced into the closed-loop system and the performance of the proportional controller in stabilizing the pattern velocity was characterized using performance measures in both the time and the frequency domain.

In Chapter 4, an adaptive gain controller is described which was used to close the loop for the fly-robot interface. External visual perturbations, similar to those presented in Chapter 3, were used to quantify the performance of the adaptive gain controller and resulting performance measures for both the adaptive and proportional controllers in stabilizing visual motion were compared.

The neural responses of the H1 cell in closed-loop were analyzed in Chapter 5 and the role of the cell in dynamically encoding the velocity and acceleration of the visual pattern motion was discussed.

Chapter 6 summarizes the results of Chapters 2-5 and provides directions for future studies to be based on the work presented in this thesis.
Figure 1.1.: (a) Self-motions of the blowfly can be described in terms of rotations (roll, pitch and yaw) and translations (thrust, slip and lift) along and around the cardinal body axes (modified from Krapp and Wicklein [2008]) (b) The major sensory systems of the blowfly are shown: the compound eyes, the ocelli and the halteres. The compound eyes are the primary visual system for the fly while the ocelli are three small eyes with a wide-angled lens arranged in a triangle on top of the head and act as a secondary visual system. The halteres are tiny club like structures that act as gyroscopes to estimate angular rotations of the fly during self-motion. Not shown in the figure are the antennae, which measure air speed and olfactory information (modified from Hengstenberg [1991]).

1.3. The Fly Visual System

1.3.1. Sensory Systems of the Blowfly

The blowfly is a member of the order Diptera and is one of the most sophisticated fliers found in the insect kingdom. During semi-tethered flight where the flight dynamics of a fly are limited, angular rotations up to 2000 deg/s have been measured in Calliphora with a top speed of 1.2 m/s and a horizontal acceleration of 2g [Schilstra and van Hateren [1999]. To control its self-motion and maintain flight stability during such rapid manoeuvres the fly relies on continuous sensory feedback. Fig. 1.1 a shows the self-motion of the fly, during unrestrained flight, as described along six degrees of freedom. The self-motion can further be classified as rotations (roll, pitch, yaw) and translations (thrust, slip, lift).
Fig. 1.1b shows the major sensory systems of the fly: the compound eyes, the ocelli and the halteres. In addition, the fly can also sense the load on the wings via mechanosensors, air-speed via antennae on the head, gravity via proprioceptors on the legs upon ground contact and head posture via neck sensory organs [Hengstenberg, 1993]. Although the blowfly is heavily reliant on its compound eyes for visual feedback for flight control and stability, it also receives complementary information about its environment from a number of other sensory modalities (review: [Krapp and Wicklein, 2008, Taylor and Krapp, 2007]). The ocelli and the halteres complement the function of the compound eyes (Fig 1.1b). The ocelli are three small eyes which together serve as a secondary visual system for the fly [Goodman, 1981]. Each ocelli consists of a wide-angled and under-focused lens. As a result of their design, the ocelli are constrained to obtaining images with very low spatial resolution and functionally they are believed to be primarily involved in sensing rotations in order to provide fast feedback for stabilization reflexes (review: [Krapp and Wicklein, 2008, Taylor and Krapp, 2007, Hengstenberg, 1993]). The halteres originate from hind-wings that have evolved into tiny club-like structures. During flight, the halteres oscillate at the same frequency as the wings but 180° out of phase. Functionally, they act as gyroscopes by measuring Coriolis forces during flight in order to provide an estimate of the angular rotation resulting from sudden attitude changes [Fraenkel and Pringle, 1938, Nalbach, 1993, Nalbach and Hengstenberg, 1994].

Both the halteres and the ocelli are involved in the inner-loop stabilization reflexes of the fly. As sensors indicating fast attitude changes of the fly, the halteres and ocelli operate with different latencies and over different dynamical ranges of motion. Ocelli provide shorter processing times (∼15 ms) for visual input as compared to the compound eyes (∼30 ms) [Parsons et al., 2006, Goodman, 1981]. Similarly, stimulating the halteres leads to compensatory head rotations observed with latencies as low 10 ms [Krapp and Wicklein, 2008].

Hengstenberg [1991, 1993] used behavioural experiments to measure the effect on the compensatory head rotations when the major sensory systems were stimulated. In doing so, Hengstenberg was able to quantify (i) the dynamic ranges over which each of the sensory systems operated at and (ii) the relative contributions of each
of the major sensory systems to the overall compensatory head movements. Hengstenberg found that the compound eyes and the halteres responded best to stimuli in the slow and fast velocity range. The contribution to head movement peaks at \( \approx 100 \, \text{deg/s} \) for the compound eyes as compared to \( \approx 1000 \, \text{deg/s} \) for the halteres (Fig 1.2). In contrast, the dorsal light response, consisting of the slow and fast responses of the compound eyes and ocelli respectively, covered a large dynamic range, with compensatory head movements observed for stimuli velocities up to \( \approx 500 \, \text{deg/s} \).

Furthermore, the overall compensatory head roll movements for gaze stabilization in the fly can be explained by the scaled linear sum of the outputs of the contributing sensory systems (Fig 1.2). The fly is therefore able to overcome the bandwidth limitations of individual sensor systems by linearly combining information across different sensory modalities. While this is true at the behavioural level, linearly combining sensory outputs is not well supported at the neuronal level because the response properties of individual neurons are highly nonlinear [Borst et al., 2003, Reisenman et al., 2003]. This simple architecture for multi-sensory integration makes the fly an ideal model system for investigating multi-sensory control at both the neuronal and the behavioural level.

The stimulus arena presented in the subsequent chapters activated the visual system via the compound eyes in an immobilized fly. While the halteres and the ocelli were not stimulated using the experimental setup, the contribution of the visual system in stabilizing the pattern motion. When interpreting and discussing the experimental results I took into account the knowledge that the fly receives complementary information regarding its self-motion over different dynamic ranges from other sensory modalities.

### 1.3.2. Organization of the Visual System

The visual space for the blowfly is defined in observer-centric spherical coordinates with the two compound eyes sampling nearly the entire visual space defined by a unit sphere (review: [Wehner, 1981]). Each of the two compound eyes of the fly is made up of approximately 7000 elements called facets or ommatidia, which are
arranged in a hexagonal lattice structure [Sukontason et al., 2008; Petrovitz et al., 2000]. Each ommatidia samples light from a distinct section of the visual space and uses a lens to focus this light onto 8 photoreceptor cells (review: Land and Nilsson [2002]). The axons of the photoreceptor cells project retinotopically onto the visual ganglia; which are comprised of three successive layers of neuropils called the lamina, the medulla and the lobula complex, with the latter being further divided into the anterior lobula and the posterior lobula plate (Fig 1.3a) (review: [Borst and Haag, 2002]). Neurons within each of the neuropils are arranged within columns and the retinotopic projection between successive layers is such that the relative position of adjacent points in the visual space is conserved throughout the visual ganglia (Fig 1.3b) ([Calliphora vicina Strausfeld, 1984], [Drosophila melanogaster Fischbach and Dittrich, 1989]).

The small size of the columnar neurons within the medulla and lobula has made it difficult to study their response properties by means of electrophysiological recordings. In contrast, visual interneurons in the lobula plate are larger (axon diameter up to 10 µm) and are therefore accessible for both intra- and extracellular recordings. There are approximately 60 different visual interneurons in each hemisphere which are collectively known as the lobula plate tangential neurons (LPTCs) (review: [Borst and Haag, 2002], [Krapp and Wicklein, 2008], [Taylor and Krapp, 2007]). Typically, most LPTCs share a characteristic response to the direction of visual motion. They are excited by motion along their preferred direction (PD) and inhibited by motion along their anti-preferred or null direction (ND). Based on their preferred orientation and dendritic arbourization patterns within the lobula plate, the LPTCs fall into one of two groups i.e. those that response primarily to horizontal motion (horizontal system or HS cells) [Hausen, 1982a] and to vertical motion (vertical system or VS cells) [Hengstenberg et al., 1982]. LPTCs can also be grouped depending on whether (i) they respond to visual motion with a graded shift of their membrane potential or by a modulation of the frequency of action potentials, or spikes, (ii) their axons project onto the contralateral lobula plate or terminate in the ipsilateral photocerebrum. The mechanisms by which visual motion is processed by LPTCs is discussed below.
1.3.3. Processing of Visual Motion by LPTCs

As the fly moves through space, it experiences panoramic image shifts across its entire eyes. These global retinal image shifts can be expressed as vector flow fields that are called optic flow. It has been proposed that optic flow provides an animal with a rich source of information regarding self-motion and distance estimation [Gibson, 1950, Koenderink and van Doorn, 1987, Nakayama and Loomis, 1974]. The self-motion of the fly along its 6 degrees of freedom (DoF) generates characteristic patterns of optic flow, which can be separated into two independent components i.e. rotation and translation (Fig 1.4a). Note that the optic flow vectors generated by both rotation and translation are in the opposite direction to that of the direction of self-motion.

Earlier work by Krapp and Hengstenberg [1996] showed that the LPTCs in flies were tuned to extract self-motion parameters from optic flow (also see Krapp et al. [2001, 1998], review: Krapp and Wicklein [2008], Krapp [2000]). Fig 1.4 shows how a cell in the vertical system is used to detect the optic flow observed during self-motion. In the example shown in the figure, the VS6 cell has a visual receptive field that is highly similar to the optic flow generated during roll rotations around the longitudinal body axis of the fly.

While global optic flow fields generated by translation and rotation self-motions of the fly are distinctly different, they cannot be distinguished from one another at the local level, (as shown by the shaded grey regions in the Mercator projections in Fig 1.4a). However, biological systems and computational methods that analyze the direction of visual motion only operate on the local level [Borst and Egelhaaf, 1993, Bulthoff et al., 1989, Lucas and Kanade, 1981, Barron et al., 1994, Horn and Schunk, 1981].

In the 1950’s, Hassenstein and Reichardt [1953] proposed the elementary motion detector (EMD) as a phenomenological model for estimating the local direction of visual motion observed by adjacent photoreceptors in the compound eyes of the fly. The EMD output model can be described as the differential sum of two identical half-EMDs, shown in Fig 1.5. A visual motion stimulus with a Gaussian light intensity distribution moving from left to right i.e. the preferred direction (PD), ac-
tivates the two neighbouring photoreceptor channels in succession. The signal from the left channel is time-delayed by a filter, $\tau$, and then multiplied by the un-delayed signal mediated by the right channel. If the time it takes the moving light intensity distribution to reach the right channel matches that of the time-delay, $\tau$, then the signals from both channels arrive simultaneously leading to a strong positive output of the half-EMD. However, a light intensity stimulus moving in the opposite direction i.e. null direction (ND) does not elicit a strong reaction from the half-EMD. The EMD model sums the differential output of two mirror-symmetrical half-EMDs to give a strong positive and negative response in the preferred and anti-preferred direction of local motion, respectively. While the sign of the EMD output predicts the direction of motion, the amplitude of the output does not represent the speed of visual motion. Instead, the EMD output is a measure of the contrast frequency, i.e. the ratio between the angular velocity and the spatial wavelength of the stimulus pattern (review: [Borst and Egelhaaf 1993]). The response properties of the LPTCs can be accurately explained as the retinotopic integration of signals from thousands of EMDs [Hausen 1984, Egelhaaf et al. 1989, Riehle and Franceschini 1984]. This integration of EMD signals is believed to be carried out by the dendrites of the LPTC cells [Single and Borst 1998].

1.3.4. Neural Control of Optomotor Response

The optomotor response is an inner-loop visual stabilization mechanism that was first discovered in the beetle Chlorophanus viridis by Hassenstein and Reichardt [1956] who observed that the animal turned in the direction of the pattern motion to reduce retinal slip speed. The optomotor response has also been observed in walking and tethered flying flies inside a rotating cylinder lined with a visual pattern (Gotz [1964, 1968a]; review: Heisenberg and Wolf [1993]). Flies under such experimental conditions have shown the tendency to turn with the motion of the cylinder with the fly able to control the optomotor response by modulating its yaw torque (cf. 1.4, this chapter). In doing so, flies reduce the visual slip speed of horizontal motion across its retinae and thus stabilize the visual input. Such stabilization mechanism helps the fly maintain a straight flight trajectory.
Previous studies have shown that the optomotor response is controlled by LPTCs responsive to horizontal motion [Geiger and Nassef, 1981; Hausen, 1982a; Hausen and Wehrhahn, 1983; Kern et al., 2005]. The receptive fields of two such LPTCs, the H1 and the HSE cells, are shown in Fig 1.6a. Both the H1 and HSE cells have receptive fields characteristic of the optic flow generated during yaw rotations around the vertical body axis.

The H1 cell is a spiking neuron that is excited by back-to-front and strongly inhibited by front-to-back visual motion, respectively. The H1 cell is one of the heterolateral neurons conveying motion information from one Lobula Plate to the contralateral one by means of action potentials [Hausen, 1982a, 1976; Krapp et al., 2001]. A fly rotating clockwise along its vertical body axis (clockwise yaw rotation) will excite its right H1 cell while simultaneously inhibiting its contralateral counterpart. Similarly, a fly undergoing counter-clockwise yaw rotation will excite and inhibit its left and right H1 cells, respectively.

The H1 cell also provides excitatory input to the HSE and HSN cells (Fig 1.6b) [Krapp et al., 2001], two major output neurons of the visual system that respond to visual motion with graded modulation of their membrane potentials [Hausen, 1976, 1982b; Hausen and Egelhaaf, 1989]. Like the H1 cell, The HSE has a response field which resembles the optic flow generated during yaw rotations, but in the opposite direction. The HSE cell is depolarised by front-to-back motion and hyperpolarized by back-to-front motion [Egelhaaf et al., 2002] and the activity of the cell is correlated with the fly’s yaw torque [Hausen, 1982b; Hausen and Wehrhahn, 1989; review: Hausen, 1993]).

The response properties and connectivity of the H1 cell make it an important neuron in the optomotor pathway of the fly. As a heterolateral neuron, the H1 cell helps disambiguate between rotation- and translation-induced optic flow. The cell is completely inhibited during forward translation but excited during yaw rotations. By connecting to the contralateral HSE and HSN cells, it makes the response of these output cells more specific to yaw rotation. The work presented in this thesis (Chapters 2-5) is based entirely on electrophysiology recordings from the H1 cell in the left visual hemisphere.
Figure 1.2.: Contributions of different sensory systems to compensatory head roll responses in *Calliphora*. In the experiments, a fly was mounted on a lightly pivoted crank attached to a servo motor such that its eyes were aligned with the horizontal and it was free to rotate its head. The crank was placed inside a cylinder, the walls of which could be lined with different patterns. Either the fly or the cylinder could be rotated, and the corresponding head rotation was recorded by a video camera. The experimental setup was used to quantify the relative contributions of the compound eyes, the dorsal light response (compound eyes and ocelli) and the halteres in the compensatory head roll movements in the fly. For the figures, the head roll (HR) is plotted against the thorax (TV) and the pattern velocity (PV), where $\lambda$ was the spatial wavelength of the pattern. (a) The fly was rolled back and forth with a sky-and-ground pattern to give the overall gaze stabilization response for the fly over the velocity range $0 - 2000$ deg/s. (b) The haltere-mediated compensatory head roll response becomes effective only at higher velocities ($> 50$ deg/s) and peaks at $\approx 1000$ deg/s. (c) Contributions to head roll by the compound eyes peaks at $\approx 70$ deg/s and decreases for lower and higher velocities. (d) The dorsal light response response is approximately constant for pattern velocities up to $500$ deg/s after which it decreases for higher velocities. The overall compensatory head roll response in (a) roughly reflects the sum of the contributions of each of the sensory systems individually stimulated during the experiments. (modified from Hengstenberg [1993]).
Figure 1.3.: Anatomical organization of the visual system of the blowfly (a) The retina, the central brain and the four visual neuropils (lamina, medulla, lobula and lobula plate) of the blowfly (modified from Borst and Haag [2002]) (b) shows the columnar retinotopic organization of the retina and the visual neuropils along with the dendritic arbourization pattern of a neuron within the lobula plate (modified from Strausfeld [1989]).
Figure 1.4.: LPTCs as matched filters for optic flow (a) The panel on the left in the top row shows the self-motion components of the fly along the 6 DoF. The panel on the right shows the optic flow fields generated during (i) pure lift translation and (ii) pure rotation along and around the vertical and longitudinal body axes, respectively, with the corresponding Mercator projections. (b) Receptive field and dendritic arbourization pattern of the VS6 LPTC shows that the cell is tuned to detect optic flow generated over the right eye during rotations around the longitudinal body axis to the left, as shown in (b)(ii). (modified from Krapp and Wicklein [2008])
Figure 1.5.: Processing local direction of motion with Elementary movement detectors (EMDs). (a) Top row shows the structure and response of the half-EMDs. The half-EMD consists of two photoreceptors attached to the ends of two channels. The left channel has a time delay \( \tau \) while the right channel is undelayed. The half-EMD output is obtained by multiplying the outputs of the left and right channels. (b) The bottom row shows that the differential output of two half-EMDs gives rise to a strong positive and negative output to visual motion in both directions (modified from Krapp and Wicklein [2008]).
Figure 1.6.: H1 and HSE receptive fields and connectivity (a) Top row shows monocular and binocular receptive fields of the H1 and the HSE LPTCs, respectively. The insets show the dendritic arbourization patterns of both cells in the left lobula plate as well as the HSN LPTC in the right lobula plate. The dendritic input arbourizations and the telodendritic output arbourizations of the H1 cell are connected via a thin axon that transmits visual motion information from the left to the right lobula plate using action potentials. The HSE and the HSN cells arbourize in the equatorial and the north sections of the lobula plate, respectively (modified from Krapp and Wicklein [2008]) (b) The interconnectivity diagram between horizontal LPTCs. Excitatory and inhibitory interactions are depicted with open triangles and filled circles respectively. The HSE and HSN LPTCs receive excitatory input from the contralateral H1 and H2. The HSE and HSN project onto descending neurons which in turn supply the neck and flight motor systems of the fly (modified from Krapp et al. [2001]).
Figure 1.7: Components of the fly optomotor response. Environmental perturbations cause visual motion across the retina of the fly. The fly is able to correct for these perturbations by compensatory motor actions in the direction of the visual motion to minimize rotation-induced retinal slip speed. At the neuronal level, the perturbations are encoded by identified visual interneurons i.e. LPTCs. The resulting neural signal is used by a controller that integrates sensory feedback and transforms the resulting command signals to the flight motor causing a compensatory body rotation in response to the perturbation.

1.4. Optomotor Responses under Closed-Loop Conditions

The individual components of the optomotor control system are shown in Fig. 1.7. An environmental perturbation, say a gust of wind, changes rotation-induced visual wide-field motion (optic flow) across its retinæ. Individually identified LPTCs analyze optic flow and encode the visual perturbations where each neuron is tuned to indicate a specific self-motion component [Krapp and Hengstenberg, 1996, Krapp et al., 1998]. The resulting neuronal signals are used by a controller which, in turn, sends a command to the actuator (flight motor steering muscles) causing the fly to compensate for the rotational perturbation.

To fully understand the optomotor response, the dynamics of the individual components i.e. the sensor, controller and actuator (Fig. 1.7), have to be characterized under closed-loop conditions. However, due to technological and methodological limitations, studies investigating the optomotor response in flies have been restricted to either a behavioural paradigm or to electrophysiology recordings from LPTCs involved in the optomotor pathway (review: Frye and Dickinson [2001]). While behavioural measurements related to the optomotor response were carried out under both open- and closed-loop conditions, the experiments involving elec-
trophysiology recordings have mostly been limited to recordings from immobilized animals under open-loop conditions. Obtaining electrophysiology recordings from a moving animal is challenging as the position of the recording electrode must remain stable with respect to the neuron being recorded from. Any relative motion between the electrode and the neuron will degrade the quality of the neuronal signal being measured. Only recently experimentalists have begun to overcome this restriction and have been able to obtain electrophysiology recordings from LPTCs in animals under less restricted conditions.

In three recent studies [Maimon et al., 2010, Jung et al., 2011, Chiappe et al., 2010], the respective authors were able to simultaneously record neural signals and well as the behaviour of the fly under minimally restrictive laboratory conditions. Maimon et al. [2010] were able to make patch-clamp recordings from genetically identified VS-cells in Drosophila, while a high-speed infrared camera was used to capture the wing kinematics of the fly during tethered flight. By correlating the neural activity of the fly during phases of rest and tethered flight, the authors found that the gain of the VS-cells was dependent on the animals locomotor state: the peak to peak response of the VS-cells was twice as large during tethered flight as compared to rest. Similarly, Chiappe et al. [2010] used two-photon imaging to monitor the intra-cellular calcium activity in the HS-cells of Drosophila while the fly was fixed in position on top of a rotating track-ball. Using the setup, the authors were able to correlate the calcium activity of the HS-cell with when the fly was walking on the trackball versus resting. Similar to Maimon et al. [2010], the authors found that the neural activity was dependent on locomotor state, such that the calcium responses were proportional to the walking speed of the fly. Subsequently, Jung et al. [2011] expanded on the work by Chiappe et al. [2010], by recording from the H1-cell in Drosophila during tethered flight. Consistent with the above studies, they found that by inducing flight using an octopamine agonist chlordimeform (CDM), the H1 velocity tuning function could be broadened as compared to when the fly was at rest. These studies illustrate the insights that can be gained into the optomotor control systems by simultaneously recording both the neural and the behavioural activity of the fly.
1.4.1. Limitations of Existing Experimental Systems

In the 1950s, Hassenstein and Reichardt used a behavioural paradigm to pioneer work on the optomotor response by using the beetle *Chlorophanus viridis* as a model system. The beetle was tethered on top of a Y-maze such that its walking motion caused a rotation of the structure. By quantitatively analysing the frequency with which the beetle turned left or right at junctions of the Y-maze with respect to the direction, contrast, spatial wavelength and angular velocity of the visual pattern, the authors were able to propose a model of the elementary movement detector (EMD) [Hassenstein and Reichardt 1956, 1953]. These seminal experiments on optomotor control in the beetle inspired similar behavioural experiments involving flies (review: [Heisenberg and Wolf 1993]). It was found that the optomotor response could be measured in tethered flying flies by using a yaw torque meter (e.g. *Musca domestica*: Fermi and Reichardt [1963]; *Drosophila melanogaster*: Gotz [1964]). In these studies, tethered flies were attached to a yaw torque meter such that they were free to perform yaw rotations around their vertical body axis. The torque meter provided a DC voltage which was in proportion to the angular momentum generated during yaw rotations. The fly and the torque meter were then placed in front of a visual display which was used to present visual pattern motion to the fly. Such an experimental setup involving measurements with tethered flies simplified studies on the optomotor responses since the behavioural activity of the fly was limited to 1 DoF and was reduced to a single variable, i.e. yaw torque. The optomotor responses of tethered flies were measured under open-loop conditions, and it was found that moving visual patterns caused an immediate yaw torque in the same direction [Gotz, 1964]. It was proposed that the fly assumes visual pattern motion as an external imposed rotation which it attempts to compensate for by generating yaw torque and counter-rotating. The yaw torque responses measured under open-loop conditions were super-imposed by torque spikes which have been identified as intended body saccades i.e. very rapid turns [Wolf and Heisenberg, 1979, Collet et al., 1993]. These torque spikes can be generated endogenously by the fly or as a result of visual pattern motion, and they complicate any input-output analysis of the fly optomotor system. While for blowflies it is not yet certain what causes the intended body saccades that generate torque spikes, it has been proposed...
that they are the result of a collision avoidance strategy [Kern and Egelhaaf [2000]. Similarly, body saccades are proposed to have a collision avoidance function in *Drosophila*, where body saccades have been caused by an expanding visual pattern in the fronto-lateral visual field of the fly [Bender and Dickinson [2006] Tammero and Dickinson [2002].

Following measurements of the optomotor responses under open-loop conditions, subsequent studies with tethered flies involved closing the loop between the visual pattern motion and the yaw torque generated by the fly (*Drosophila melanogaster*: Heisenberg and Wolf [1988], Wolf and Heisenberg [1979], Heisenberg and Wolf [1984]; blowfly *Lucilia*: Warzecha and Egelhaaf [1996], Kern and Egelhaaf [2000]). Closed-loop experimental setups are often referred to as a "flight simulator" since the effect of the fly's motor activity, in this case its yaw torque, directly influences the angular velocity of the visual pattern presented to the fly. To close the loop, the fly's angular velocity was estimated from its yaw torque by scaling the latter by a fixed coupling coefficient [Reichardt and Poggio [1976]. The fly's estimated angular velocity was then subtracted from the angular velocity of the pattern under real-time closed-loop conditions. Within the closed-loop flight simulator, the fly maintains a state of optomotor equilibrium; it is able to modulate its yaw torque in order to stabilize its visual surroundings. The feedback controller used to close the loop for the flight simulator is equivalent to a proportional feedback controller with a fixed or static feedback gain.

It should be noted that the coupling yaw torque to the angular velocity of the visual pattern is not the only way to close the loop within a flight simulator. Visual stimulation of the fly has been shown to alter the wing beat amplitude as well as the forward torque [Gotz [1968b]. The fly is able to control yaw torque by modulating its differential wing-beat amplitude (ΔWBA) [Gotz [1987] Fry et al. [2003] and its forward thrust by modulating both the wing pitch and total force magnitude [Fry et al. [2005]. Both the wing-beat amplitude [Chow and Frye [2008], Graetzel et al. [2008] and the forward torque [Wolf et al. [1992] have been previously used as behavioural feedback signals in order to close the loop between the fly’s motor output and the visual input it perceives.

Furthermore, optomotor responses have been shown to have a high degree of flex-

34
ibility, in that the fly can also use the differential activity of its front legs movements as a feedback signal to stabilize the observed pattern motion inside a flight simulator [Wolf et al., 1992]. A more recent study carried out by Graetzel et al. [2008] in *Drosophila melanogaster* further highlights the flexibility of the optomotor response. The authors developed an experimental system which allowed them to measure, in real-time, the wing kinematics of a fly in tethered flight [Graetzel et al., 2006]. The wing kinematics were fed into a Kalman filter to estimate the yaw, lift, and thrust response of the fly, which were in turn used by a control law to generate motor commands to control the movement of a mobile robot. The authors found that when the activity of the fly was coupled to the robot using a naturalistic feedback strategy, (i.e. yaw response of the fly coupled with yaw response the robot, lift/thrust of fly coupled with the robot's forward velocity) the robot was able to navigate a cluttered environment without colliding with obstacles. Even when a completely artificial feedback strategy was used (i.e. the fly's lift response used to control the robot's turning response), the robot was still able to navigate its environment without collisions.

The flexibility of the optomotor response has allowed experimenters to use systems identification approaches to study the control strategies underlying optomotor control in the fly. Recently, Theobald et al. [2009] measured the wing kinematics (ΔWBA) of a fly under tethered flight while the optic flow fields it experienced were varied systematically about the three cardinal axes. By correlating the visual images observed by the fly with the fly's lift and thrust responses under open-loop conditions, the authors were able to obtain linear finite impulse response (FIR) filters for each optic flow field. The authors found that each flow field had a unique FIR filter associated with it. Furthermore, the linear filters explained a large proportion of the total response variance in the fly's behaviour (≈ 75%), indicating that the optomotor response was driven, to a large extent, by a linear control system. In a similar study, Graetzel et al. [2010] used vertically oscillating visual patterns and measured the ΔWBA to approximate the lift response in *Drosophila*. The authors found that the lift response in the fly, like the response to optic flow fields, was predominantly linear and time-invariant, further suggesting that visuo-motor control strategies are largely linear at the behavioural level. Not only have experimentalists been able to use system identification approaches to investigate optomotor control
during tethered flight, they have been able to use these techniques during free-flight conditions as well. Fry et al. [2008] designed a wind tunnel equipped with both a 3D path tracking system and a virtual reality display lining the walls. Using the system they were able to systematically alter the spatial and the frequency tuning observed by the fly in combination with its corrective responses, as the fly navigated through the wind tunnel. By decoupling the pattern velocity observed by the fly to its flight speed during free-flight, Fry et al. [2009] were able to estimate the open-loop transfer for the visual control of flight speed and reported that it depends on the linear pattern velocity \( v = \text{temporal frequency/ spatial frequency} \). In a related subsequent study, Rohrseitz and Fry [2010] used the wind tunnel setup described above to measure both the open- and closed-loop transfer functions which explain the flight speed from the visual perturbations observed under free-flight conditions. The authors found that the transfer functions remain unchanged during open- and closed-loop conditions, an observation that was in contrast to the dissimilarity in yaw torque responses measured under open- and closed-loop conditions during tethered flight [Heisenberg and Wolf, 1988].

In all these cases, the optomotor response is studied at the behavioural level, where only the compensatory motor action in relation to the visual slip speed can be measured and thus the red dotted box in Fig. 1.7 remains a black box. Heisenberg and Wolf [1993], distinguished physical torque from neural torque in the control of the optomotor response. The latter refers to the neuronal signal sent to the flight motor while physical torque is a measure of the output it generates. An injury to one or both of the wings might require the fly to increase or decrease its neural torque in order to maintain its optomotor equilibrium. While the physical torque generated during the optomotor response has been extensively studied, the control strategies by which the neural torque is used are poorly understood. In the case of the FRI, the yaw rotation of the robot and the visually mediated neural activity of the H1-cell represent the physical and neural torque, respectively.

In order to understand how the activity of the LPTCs sensitive to horizontal motion (cf. Section 1.3.4, this chapter), is used to control motor action, studies have focused on obtaining electrophysiology recordings from the LPTCs while the fly is stimulated using a visual display. Frye and Dickinson [2001] have categorized
these electrophysiology studies into three experimental paradigms.

The first experimental paradigm involves visual stimulation of an immobilized fly using a cathode-ray tube (CRT) display that covers a large area of its visual field while intra- or extracellular recordings are made from individual LPTCs e.g. Egelhaaf and Reichardt [1987]. A modification to this approach was used by Krapp and Hengstenberg [1996, 1997] to visually stimulate small patches of the fly visual field in order to recover the local sensitivity and direction selectivity to visual motion within the receptive fields of LPTCs. Traditional electrophysiology experiments have been invaluable in revealing the functional role of the LPTCs in modulating the optomotor yaw response (e.g. Hausen [1982a,b]; review: Hausen [1993]).

In those studies, however, flies were presented with artificial or synthetic motion stimuli. While such artificial motion stimuli can be used to mimic certain self-motions of the fly, e.g. yaw rotations, during free flight the animal experiences complex optic flow that is a combination of both rotation- and translation-induced components. In order to overcome these restrictions, so-called "replay experiments" [Heisenberg and Wolf, 1993] were introduced to provide naturalistic visual input to the fly, as observed during free flight conditions. These replay experiments involved the following general steps (i) monitor the movements of a tethered or freely flying animal inside a visual arena, (ii) reconstruct and replay the visual motion generated as a result fly’s self-motion on an CRT display and (iii) obtain electrophysiology recordings from an immobilized fly placed in front of the CRT display.

The second and third experimental paradigms defined by Frye and Dickinson [2001] are both variants of these replay experiments. The first set of replay experiments were performed by Kimmerle et al. [2000] and Kimmerle and Egelhaaf [2000] where a tethered fly was fixed inside a cylindrical arena lined with LED panels. Similar to the behavioural closed-loop flight simulator experiments described above, the yaw torque of the fly controlled the angular velocity of the visual pattern displayed on the LEDs. The authors stimulated the fly with a small object moving relative to a textured background and recorded the visual images observed by the fly under closed-loop conditions. These images were then played back to an
immobilized fly in front of an electronic display while electrophysiological recordings were made from the FD (figure detection) and HS LPTCs. In doing so, the activity of the LPTCs could be correlated with the visual input generated as a result of the self-motion of the fly under closed-loop conditions.

The restrictions imposed by tethered flight limits optic flow generated from the self-motion of the fly to purely rotation components. In order to investigate neural coding of translation components, Kern and Egelhaaf [2000] used a video capture system to film the movements of a monocularly blinded fly walking inside a visual arena. The video images were used to determine the trajectory of the fly and the authors found that it was difficult to observe any differences in trajectories between monocular blinded and binocular flies. The trajectories were used to reconstruct the visual motion observed by the monocularly blinded fly inside the visual arena which in turn was replayed to the fly while electrophysiological recordings were made from the HSE cell [Kern et al., 2000]. The behavioural and electrophysiology experiments confirmed that the fly attempts to maintain optomotor equilibrium by following a trajectory that balances the rotatory and translation components of the observed optic flow.

Further studies improved upon the replay experiment paradigm by reconstructing the optic flow observed by the fly during free flight [Kern et al., 2005]. The magnetic search coil technique pioneered by Schilstra and van Hateren [1998a,b] was used to obtain the head and body positions of the fly while flying inside a visual arena the walls of which were lined with naturalistic images of herbage. The study suggested a second function for the HSE cell. While previously thought to only encode yaw rotations around the vertical body axis (e.g. [Krapp et al., 2001]), the study suggested that the HSE cell also used the time interval between body saccades to estimate relative distances from the translation-induced optic flow components. Other improvements to the replay experiment paradigm involved using sophisticated visual displays such as a mechanical wide-field projector [Karmeier et al., 2003] and a wide-field LED stimulator called the Flimax [Lindemann et al., 2003].

In all the replay experiments described above, electrophysiology recordings were made under laboratory conditions where the visual stimuli were limited to grat-
In order to overcome this restriction, Lewen et al. [2001] performed challenging experiments involving electrophysiology recordings on a moving platform. In the study, an immobilized fly was mounted onto a turntable rotating around the vertical axis while electrophysiology recordings were made from the H1 cell. The turntable was placed outside the lab environment, in a wooded area. By precisely controlling the rotation velocity of the turntable the responses of the H1 cell could be obtained under nearly naturalistic visual stimulation conditions. The authors found that under outdoor conditions the temporal precision at which the H1 cell generated spikes in response to the visual stimulus was way higher than previously reported, i.e. at the sub-millisecond level.

In addition to the electrophysiology and the behavioural experiments, modeling work and robotic controllers have been combined to understand the control principles underlying closed-loop optomotor control in flies. Lindemann et al. [2008] used computer simulations in which the differential output of two HSE cells was used to control the yaw torque of a cyberfly within a virtual flight simulator. When the activity of one of the HSE cells exceeded a predefined threshold value, a body saccade was imposed upon the trajectory of the cyberfly. The modeling work showed that a saccadic controller helps the fly avoid collisions during free flight (also see: Stewart et al. [2010]). However, as argued by Webb [2006, 2000, 2001] using pure modeling studies to understand animal behaviour has limitations in that the computer model has no real-world physical interactions. The lack of physical interaction would mean that complex motion dynamics such as slippage due to temporally reduced friction couldn’t be accounted for in the computer model. Indeed, recent work by Dickson et al. [2010] used a scaled robotic model to suggest that both body-inertia and -damping play a significant role in the dynamics of saccadic turns during free-flight of Drosophila. Such motion dynamics remain unaccounted for in pure modeling studies on optomotor control.

Overcoming these limitations, Franceschini et al. [1991] assembled EMD sensors in silico to mimic signal processing properties of the fly visual system. The sensor was placed on an autonomous mobile robot to perform collision avoidance tasks. Similarly, Webb et al. [2004] and Harrison and Koch [2004] used a silicon implementation of the fly’s visual system (see Harrison and Koch [2000]) in order
to build a robotic optomotor controller with 1-DoF for a collision avoidance task. The study by Reiser and Dickinson [2003] provides the most sophisticated robotic implementation of the fly optomotor system. The experimental system consisted of a video camera mounted inside a cylindrical arena lined with a textured pattern. The motion of the video camera was controlled by a robotic gantry system with 5-DoF. A control system was designed that used visual (saccadic controller similar to that used by Webb et al. [2004], Lindemann et al. [2008]) and mechanosensory (haltere) signals for feedback control. The results with the controller were in agreement with the behaviour of Drosophila observed within a visual arena under free-flight conditions.

In their study using the 5-DoF fly controller, Reiser and Dickinson [2003] noted that the most significant limitation of their study was the lack of appropriate performance metrics related to behavioural tasks such as obstacle avoidance. A solution to this limitation potentially comes from recent studies where experimentalists have begun to use system identification tools, such as step and frequency response characterization, in order to quantify the performance of visuo-motor tasks in the fly (lift response in Drosophila: Graetzel et al. [2010]; optomotor response in Drosophila: Theobald et al. [2009]; head roll compensation in Calliphora: Schwyn et al. [2011]).

All the studies reviewed above consist of experimental systems where either the behavioural or the neural activity of the fly can be measured but not both simultaneously. Similarly the robotic studies are limited in that their sensory stages are based on a silicon implementation of the flies visual system which fails to capture the nonlinear effects of motion adaptation along the visual processing pathways in the fly [Maddess and Laughlin, 1985]. In contrast, the modeling studies fail to provide real-world physical interactions.

So far, the only study involving the measurement and use of neuronal signals for optomotor control was carried out by Warzecha and Egelhaaf [1996]. Recordings were made from both the ipsi- and the contralateral H1 LPTCs in an immobilized fly while it was visually stimulated by a moving grating presented on a CRT display. The differential activity of the two H1 cells was used to control the angular velocity of the moving pattern for different feedback gains. The study showed that gain
control properties of the EMDs prevented the optomotor response from becoming unstable. While the study carried out by Warzecha and Egelhaaf [1996] was unique in that it allowed for the simultaneous measurement of the yaw torque and the neural activity under closed-loop conditions, the subsequent analysis was based completely on steady state responses. A steady state analysis, however, does not capture the complete dynamic properties of the underlying control system, such as transient responses to the onset of a stimulus, damping coefficients or oscillatory response components, and the speed at which the visual perturbation is corrected for [Collet et al., 1993].

Referring back to the distinction made by Heisenberg and Wolf [1993] between physical torque and neural activity, while the physical torque generated during the optomotor response has been extensively studied, the control strategies by which neural activity is transformed into the physical torque are poorly understood. To address this problem an experimental system is needed that (i) allows for the simultaneous measurements of both the visually-mediated neural (H1-cell) and the corresponding behavioural activity of a motor system (in this case the robot controller) generated during the optomotor response, (ii) allows for testing different feedback control strategies, (iii) includes real-world physical interactions and (iv) where the data analysis is based on appropriate performance metrics that take into account the dynamics of the optomotor system studied.
In the previous chapter, the methodological restrictions of existing experimental systems for investigating visuo-motor control in flies were discussed and an argument was made for an experimental system where simultaneous measurements of both behavioural and neural activity can be obtained while a fly performs a visual stabilization task under closed-loop.

In this chapter, a novel closed-loop experimental system consisting of a fly-robot interface (FRI) is described. The FRI allows for simultaneous closed-loop measurements of both neural activity and behavioural performance. The technical specifications of the individual components of the experimental system are described in detail and the data analysis methodology is presented along with a concluding discussion on the overall design of the fly-robot interface.

2.1. Design of the fly-robot interface

The experimental system consisting of a fly-robot interface (shown in Fig 2.1) was designed to be a closed-loop flight-simulator for the fly. An immobilized fly was placed in front of a visual display consisting of two high-speed cathode-ray tube (CRT) computer monitors. Input to the two computer monitors were provided by two high-speed video cameras mounted on a small, two-wheeled customized mobile robot (cf. section 1.1.1). The robot was positioned on a turn-table within a
Figure 2.1: Experimental design for the closed-loop visual stabilization task with the fly-robot interface. The control loop operates in the direction specified by the arrows in red. A robot is mounted on a rotating turn-table which is placed inside a visual arena. The walls of the arena are lined with a vertically oriented grating pattern. The relative motion between the robot and the turn-table is captured by two high speed cameras mounted on the robot and the visual images are transmitted to the high-speed monitors in front of the fly. Electrophysiology recordings are made from the H1 cell in the left visual hemisphere of the fly. The spiking activity of the H1 cell is used to estimate the spiking rate and compute an updated compensation speed for the robot. Based on the estimate of the compensation speed, the robot accelerates or decelerates in order to compensate for the imposed motion of the turn-table.

cylindrical arena whose walls were lined with a pattern of vertically oriented, black and white stripes. Any visual motion as a result of the rotation of the turn-table was captured by the two cameras and displayed on the two CRT monitors in front of the fly. Electrophysiology recordings were made in the immobilized fly from the H1 cell, an identified visual interneuron that is responsive to back-to-front visual motion e.g. [Krapp et al., 2001]. Visual motion presented on the CRT monitors caused spiking activity in the H1 cell. This spiking activity was recorded, filtered and used to control the rotation of the robot on the turn-table.

In the closed-loop system described above, the fly along with its H1 cell was used as a sensor that provides an estimate of the horizontal angular velocity of the visual pattern. The robot and the turn-table with their dynamic properties represent the
real-world actuator components where the latter was used to introduce visual perturbations into the closed-loop system. The relative motion between the robot and the turn-table mimic the movements of the animal which result in horizontal visual motion.

The turntable and robot were set up to rotate in opposite directions. The turntable was restricted to counter-clockwise rotations only. This was done so that the rotation of the turntable resulted in visual motion in the preferred direction of the H1-cell (Fig 2.5a). In comparison, the robot was restricted to clockwise rotations only, which allowed it to compensate for the rotation of the turntable thereby minimizing the visual pattern motion observed by the fly. Perfect compensation was achieved when the turn-table and robot angular velocities were equal and there was no observed visual pattern motion.

The angular velocity measurements from the robot and the turn-table were logged along with the electrophysiology recordings of the H1 cell thus providing simultaneous measurements of the robot’s performance and the neural activity. The technical configuration and characterization of the subsystems of the FRI are described in detail in the following sections.

2.1.1. Dynamics of Experimental Robotic Platform

In order to investigate opto-motor control principles, a mobile robot was chosen to provide real-world motion dynamics for the fly-robot interface. A number of commercial robotic platforms were considered namely the Khepera, LEGO Mindstorms NXT and the ASURO robot. The Khepera, while widely used would not have been able to support the weight loading requirements of the experimental system. The LEGO Mindstorms NXT, while very popular, was unsuitable since it has a 30 ms delay in switching between transmission and receiver mode while communicating through it’s Bluetooth module. This would imply a minimum of 60 ms control loop delay in sending and receiving information from the robot alone, not taking into consideration the additional time required for processing on the robot.

Given the design specifications of the fly-robot interface, the ASURO mobile robot came closest and was chosen as a platform of choice. The ASURO is a small
mobile robot that is built with off-the-shelf components (Fig 2.2a). At its core is an Atmel ATmega8 (RISC) microprocessor that can be reprogrammed in C (WinAVR/GNU GCC tools for Microsoft Windows). Two DC motors drive the robot and its caster wheel design enables it to turn on the spot. Shaft encoders measure the rotation of the two wheels.

Several customizations were made to the ASURO robot. With its factory design, two way communications was possible by way of infra-red transceivers which resulting in line-of-sight restrictions. To circumvent this problem, the IR transceiver on the ASURO PCB was disconnected and the RX (serial receive) and TX (serial transmit) pins on the micro-controller were connected to a serial Bluetooth modem (Sparkfun - Bluesmirf). The Bluetooth module was powered by the onboard robot power supply and was configured to communicate with a PC with the following parameters: Baud Rate - 2400 Bits, Data-bits - 8, Parity - none, Stop-bits - 1, Flow control - none. The optional wireless mechanism for reducing frame packet collisions (RTS, ready to send/CTS, clear to send) was not used.

![Figure 2.2: ASURO Robot before (left) and after (right) custom modifications. A chassis was assembled on top of the robot in order to mount two high-speed cameras and battery pack. Separately, a serial Bluetooth module was mounted towards the front end of the robot.](image)

To sample the visual motion as a result of the movement of the robot in space, two high-speed cameras (Prosilica GC640) were mounted on the ASURO. The cameras were chosen because they were able to achieve the high-frame rates necessary in order to correctly stimulate the H1 cell in the fly (cf. Visual Stimulation of the H1
The cameras were mounted such that their optical axis were perpendicular with respect to each other and the vertical axis of rotation of the robot. Each camera was capable of capturing images at 200 frames/s at a resolution of 640 x 480. 6 mm C-mount lens on each camera sampled a visual space of 41.2° horizontal and 51.9° vertical angles respectively. The image acquisition of the cameras were synchronized by operating them in master-slave mode. The master was configured to acquire images at a fixed frame rate of 200 frames/s. The master was also daisy-chained to the slave camera via a physical trigger. Each image acquisition event at the master camera, triggered a similar image acquisition event for the slave camera, effectively synchronizing the two devices.

The robot was mounted on the turn-table such that the axis of rotation of both coincided with each other and that both were free to rotate independently along the vertical axis. To mount the robot on the turn-table, a small hole was drilled in the chassis which coincided with the robot’s axis of rotation. A corresponding axle was vertically mounted in the center of the turn-table which slipped over the hole in the robot chassis and held it firm in place and confined its movements to rotations around the vertical axis.

**Motion Control & Dynamics**

The motion of the robot is controlled by two DC motors on either side with the robot designed to do point turns due to a caster wheel at the front of the chassis. The motors control the wheels using a dual-stage gear (gear ratio 12:5). The motors were set to rotate with the same speed in opposite directions and their speed was set by an 8-bit input value, \( V_r \in \{0, 1, \ldots, 255\} \). Wheel revolutions were measured using optical encoders mounted close to the axle. Given the gear ratio, the diameter of the wheel (38 mm) and the diameter of the path required for one complete rotation of the robot about a point (103 mm), the angular velocity (in degrees) of the robot, \( \omega_r \), was calculated from the optical encoder values as:

\[
\omega_r = \frac{\text{encoder clicks}}{\text{Path Diameter}} \cdot \frac{\text{Wheel Diameter}}{\text{Gear Ratio}} \cdot \frac{360}{\text{dt}}
\]  

(2.1)
where, encoder clicks are the digital readings from the optical encoders obtained within a time period $dt$.

To estimate the relationship between the input speed value $V_r$ and the angular velocity of the robot $\omega_r$, the robot was made to rotate about a point in the clockwise direction for $150 \leq V_r \leq 250$ and the mean and standard deviation were calculated over 10 second intervals. The relationship between $V_r$ and $\omega_r$ is shown in Fig 2.3. For $V_r \leq 160$, the robot is unable to move due to stalling of the motors as a result of weight loading of the cameras and batteries. As a result, for $V_r \leq 160$ the angular velocity, $\omega_r$, is zero. As $V_r$ increases from 160 to 170, the robot is able to overcome its weight loading, which results in a notable jump in angular velocity ($\omega_r \approx 50$ deg/s). For the range $170 \leq V_r \leq 250$, an approximately linear relationship exists between $V_r$ and $\omega_r$ with the standard deviation remaining approximately constant between $\pm 10 − 15$ deg/s.

Furthermore, the dynamics of the robot were characterized by its frequency response. Sinusoid signals with different input frequencies were used as input speed values for $V_r$ and the corresponding angular velocities $\omega_r$ were measured. The values for $V_r$ were modulated between the range $[150 − 250]$ within a frequency range...
of 0.03 – 3.0 Hz. The resulting Bode magnitude and phase plots are shown in Fig 2.4. Details on how the Bode plot was calculated are given in the Data Analysis Methods section later on in this chapter.

![Robot Bode Magnitude](image1)

![Robot Bode Phase](image2)

**Figure 2.4:** Frequency response characterization of the robot rotation calculated over N=10 trials. The mean and standard deviation of the Bode (a) magnitude and (b) phase plots are shown. Both the gain and phase decrease with increasing frequency, suggesting a low-pass filter characteristic for the horizontal rotation of the robot.

The Bode plots for the horizontal rotation of the robot (Fig 2.4) show a low-pass filter characteristic typical of a mechanical actuator system. The power of the output signal of a low-pass filter is maximal at the frequency with the highest system gain ($G_{dc}$). A low-pass filter is also defined by its operating bandwidth. The bandwidth for a low-pass filter are the range of continuous frequencies over which the power of the filter output signal is greater than $\frac{1}{2}$ the power at $G_{dc}$. The drop in power by $\frac{1}{2}$ corresponds to a drop of 3 dB in the system gain relative to $G_{dc}$. The cut-off frequency $f_c$ is defined as the frequency at which the system gain first drops below $G_{dc} - 3$ dB. For a low-pass filter the bandwidth is equivalent to the cut-off frequency $f_c$ Hz. From the Bode magnitude plot of the robot, the cut-off frequency is approximately $f_c = 0.5$ Hz. Since the frequency response for the robot is calculated over the frequency range 0.03 – 3 Hz, the highest system gain, $G_{dc}$ is $6.38 \pm 1.41$ (mean±sd) and the resulting bandwidth is approximately 0.47 Hz.

From the frequency response shown in Fig 2.4, the transfer function, $G(s)$, between $V_r$ and $\omega_r$ for the horizontal rotation of the robot was estimated as (see Data
Analysis Methods section for derivation):

\[ G(s) = \frac{1.73}{s^2 + 1.87s + 0.86} \]

For the estimated transfer function, \( G_{dc} = 1.73 \) while the bandwidth is slight higher at 0.58 Hz.

In comparison, the bandwidth for the H1-cell in the fly is approximately 12 Hz \([\text{Borst} 2003]\). However, the limiting factor for optomotor control in the case of flies is the flight motor system. In behavioural studies, Egelhaaf (1987) visually stimulated \textit{Musca domestica} with oscillating patterns and observed that the yaw torque had low-pass filter characteristic. For low input frequencies, \( f_i \leq 0.0625 \) Hz, the measured yaw torque was approximately constant. However, increasing the input frequency beyond 0.0625 Hz resulted in the yaw torque declining approximately linearly. Beyond \( f_i = 4 \) Hz, the measured yaw torque response was nearly zero.

### 2.1.2. Turn-table for Introducing External Visual Perturbations

While the robot is used to provide real-world motion dynamics for the fly-robot interface, the turn-table which the robot is mounted on is used to introduce a rotation bias within the closed-loop system. This rotation bias causes external visual perturbations within the closed-loop system which are then compensated against by the fly.

The turn-table consists of a circular metallic plate connected to a stepper motor (Sanyo Denki, 103H6704-0140, uni-polar winding). Similar to the robot, the turn-table is limited to rotation about its vertical axis and its angular velocity \( \omega_p \) is controlled via a micro stepper drive (Applied Motion Systems, ST5-SI).

Figure 2.5 shows a cartoon of the relative motion between the turn-table and the robot. The turn-table is placed within a cylindrical arena (Fig 2.5b) the walls of which are lined with a vertically oriented grating pattern (Spatial wavelength \( \lambda_{sp} = 11^\circ \), contrast \( \approx 100\% \)). The spiking-rate of the H1-cell is a maximum for a stimulation contrast frequency (image velocity/spatial wavelength) between 2-4
Figure 2.5.: Configuration of experimental setup (a) The turn-table is rotated counterclockwise while the robot compensates for the imposed motion in the clockwise direction. When the relative motion between the turn-table and the robot is such that $\omega_p > \omega_r$, the visual motion is the preferred direction (PD) for H1 and the cell is stimulated. For $\omega_p > \omega_r$, the visual motion is in the cell’s anti-preferred or null direction (ND) and the neuron is inhibited. (b) The walls of the cylindrical arena are stationary while the turntable is free to rotate along its vertical axis (c) Position of the robot on top of the rotating turntable.

Hz [Warzecha et al., 1999] and the spatial wavelength was chosen such that the contrast frequency under closed-loop conditions was close to this optimal value. So that in order to stimulate the H1 cell by means of horizontal motion which coincides with the neuron’s preferred direction (PD) (see Fig 2.9), the turn-table is made to rotate in the counter-clockwise direction. The robot is required to compensate for the imposed external visual perturbation as a result of the turn-table,
and does so by rotating in the opposite i.e. clockwise direction (Fig 2.5c).

**Motion Control & Dynamics**

The turn-table angular velocity $\omega_p$ is controlled via voltage signal, $V_p$, between $\pm 5$ V. A circular grating pattern is printed underneath the turn-table surface and a photodiode is mounted 2.5 cm from its surface.

With complete robot weight loading, the relationship between $V_p$ and $\omega_p$ is highly linear as shown in Fig 2.6. Furthermore, the standard deviation is below $\pm 8$ deg/s which is smaller than the largest system error involved in attempting to visually align the head in different blowflies with the stimulus display [Petrovitz et al., 2000].

![Figure 2.6](image)

**Figure 2.6.** (a) Linear relationship between the input voltage $V_p$ and the steady state angular velocity $\omega_p$ for the turn-table (b) Standard deviations in trying to maintain a constant speed for the turn-table decrease with increasing $V_p$.

Similar to the robot, the frequency response was calculated for the turn-table over the frequency range $0.03 – 3.0$ Hz with a peak amplitude of 144 deg/s. The Bode magnitude plot (Fig 2.7a) also shows low-pass filter characteristic. The frequency cutoff $f_c = 3.0$ Hz for the turn-table is however much higher than that compared to the robot. Additionally, the input-output phase difference is also very low with a peak difference of approximately $20^\circ$ at $f = 3$ Hz. As a result, the turn-table does not significantly not limit the dynamic range of the closed-loop system and is
therefore suitable to introduce external visual perturbations in the frequency range 0.03 – 3.0 Hz.

![Turn-table Bode Magnitude](a)

![Turn-table Bode Phase](b)

Figure 2.7.: Frequency response characterization of the turn-table rotation calculated over N=10 trials. The mean and standard deviation of the Bode (a) magnitude and (b) phase plots for the rotation horizontal of the turn-table over the frequency range 0.03 – 3.0 Hz.

2.1.3. Visual Stimulation of the H1 Cell

The visual pattern motion resulting from the relative motion between the turn-table and the robot was captured by two high-speed cameras mounted on the robot (for details see sub-section on the Mobile Robot). The images from each camera were displayed on a CRT screen (LG Studioworks 221U) capable of refresh rates up to 200 frames/s at a resolution of 640 x 480 and controlled by a graphics card (NVIDIA Quadro NVS 285). As shown in Fig 2.8a, the CRTs were positioned such that the mid-sagittal plane of the fly and the center of the CRTs span a horizontal angle of 45° (see [Warzecha and Egelhaaf, 1997]). The monitors were also adjusted so that the screens were perpendicular to the horizontal plane defined by the fly’s eye equator and such that they individually covered an angle of 50° horizontal and 38° vertical in each visual hemisphere of the fly.

Software was written in C++/OPENGL using the proprietary HERMES library (Norpix) to synchronously capture and display images from the cameras on the
CRT monitors. The camera triggering did not cause any delay in the acquisition and display of images from the camera on to the CRT monitors. Separate threading was used for the image acquisition and display events to reduce the bottleneck in the capture and display of images. A separate PC (Operating system: Microsoft Windows) was used for each camera/monitor configuration with hard drives in each PC configured to Raid 0 operation mode (striped volume mode) in order to increase data write speeds. For each image acquired by the camera, the raw uncompressed image was saved along side the display times.

The CRT image display times were measured during a 30 second test. The mean and standard deviation of the image timestamps were close to the desired 200 frames/s refresh rates (5.02 ± 0.94 ms). The CRT monitors were covered with a metal mesh which in turn was connected to a grounding block. This was done to reduce the effect that the electromagnetic fields generated by the monitors had on the electrophysiology recordings from the H1 cell (Fig 2.8b).

Using a CRT monitor to visually stimulate the H1 cell may cause artifacts in the electrophysiology responses and must be accounted for. Kern et al. [2001] used a CRT monitor to stimulate the HSE cell in Calliphora (100 Hz frames/s) and found that the electrophysiology responses were time-locked to the image presentation (flashing) of the monitor. The time-locking of the electrophysiology response is a
result of *Calliphora* having a very high flicker fusion frequency (FFF) of approximately 250 Hz [Autrum, 1958]. Visual stimulation at a frame rate below the FFF causes the frames to be perceived as individual images as opposed to smooth motion. The FFF itself is not static, but is dependent on the overall light intensity, with higher and lower light intensities increasing or decreasing the FFF, respectively [Miall, 2008].

To determine whether the CRT monitor in the experimental setup caused time-locking of the H1 cell, the cell’s electrophysiology responses were cross-correlated with the image presentation times. Electrophysiology recordings were made from the H1-cell while the CRT monitor was used to display a static vertical grating pattern to the fly for a duration of 40 s. The H1 spike rate and image presentation times were sampled at a resolution of 1 ms and the cross-correlation between the two signals was calculated. The cross-correlation was averaged over N=6 flies. If the image presentation times affected the spike rate of the H1 cell, there would be a high correlation in the cross-correlation sequence and a low correlation otherwise. A very low correlation of 0.093 ± 0.004 (mean±sem) was observed at delay of 4 ms, confirming that the camera/monitor visual stimulation setup did not introduce time-locking artefacts in the response of the H1 cell.

### 2.1.4. Blowfly *Calliphora* as a Sensor for Visual Pattern Motion

As introduced earlier in Chapter 1, the H1 cell is an identified visual interneuron in the lobula plate of the fly. The H1 cell is a spiking neuron, that is excited by back-to-front (Fig 2.9) and strongly inhibited by front-to-back visual motion. The response of the H1 cell can be characterized by its spiking rate. When there is no visual motion, the cell responds with a spontaneous spiking rate $F_s$. When presented with visual motion with optimal stimulus parameters in its preferred direction (pattern contrast frequency = 2 – 4 Hz), the cell responds with a peak spiking rate $F_{\text{max}}$. When presented with visual motion in its anti-preferred direction, the cell is highly inhibited and the spiking rate quickly drops to 0 Hz. As a result of its response properties, the H1 cell is perfectly suited as a yaw rotation sensor for the closed-loop experiments involving the stabilization of visual motion along the
Dendritic arbourization and response field of the H1 tangential cell. The cell is stimulated by horizontal motion in the back to front direction. The cell has peak sensitivity between $\pm 15^\circ$ elevation. Image taken from [Krapp et al., 2001].

horizontal plane.

**Fly preparation and electrophysiology recordings**

Flies were immobilized to prevent any body or head movements from corrupting the stability of the neuronal recordings and the head was correctly oriented with the visual stimulation equipment. A 2-3 day old female blowfly *Calliphora* was cooled on ice, and it’s back fixed to a piece of double-sided tape on a microscope slide. The legs, wings, and proboscis were removed and the holes covered with beeswax. The fly was then mounted on a custom holder which allows for correctly orienting its head with respect to the visual stimulation displays. An optical phenomenon called the pseudo-pupil can be observed in each eye when viewed under a microscope with red light. The pseudo-pupil was used to align the fly’s head with the stimulus [Franceschini, 1975]. The fly was then firmly fixed to holder by waxing down the head and thorax. A micro-scalpel was used to cut small windows into the cuticle of the back of the left and right head capsules and forceps were used to remove any floating hairs, fat deposits or muscle tissue that may cover the lobula plate.

Tungsten electrodes (signal & ground, fh-co.com, Item code - UEW SHG SE
3P1M) were used to record extracellularly from the H1 cell in the left head capsule of the fly. The signals from the H1 cell were amplified (NPI EXT 10-2F, gain - x 10k) and band-pass filtered between 300-2k Hz. The resulting signals were sampled using a data acquisition card (National Instruments USB 6215, 16-bit) at 10 kHz. The electrophysiology signals of the H1 cell were used for closed-loop control and were also stored on the hard disk for offline analysis.

### 2.1.5. The Control Loop

![Block diagram](image)

**Figure 2.10.:** Block diagram for the closed-loop fly-robot interface shows the three primary components: the sensor (fly H1 cell), the controller and the actuator (robot).

Fig 2.10 shows the block diagram for the closed-loop experimental system. The primary components of the system have been described in the sections above. The turn-table is rotated at an angular velocity $\omega_p$ which introduces external visual perturbations into the closed-loop system. This visual motion, or slip speed, is observed by an immobilized fly while electrophysiology recordings are made from its left H1 cell. The cell responds with a spike rate, $F$, which is used by a controller to compute an update speed, $V_r$ for the robot that is converted into an angular velocity $\omega_r$ to close the loop.

The processing of the data required to setup the control loop was implemented as a program written in Matlab (version R2010a, Mathworks Inc.). The hardware clock on the data acquisition card was used to generate a timer event every 50 ms which synchronized the electrophysiology recordings with the data processing routines. The value of the control loop update rate (50 ms) was constrained by two factors. The update rate had to be large enough to allow for (i) error free data transmission
over the Bluetooth interface and (ii) the estimation of the smoothed spike rate, $F$. A screen-shot of the diagnostic section of the software is shown in Fig 2.11. Each timer event triggered the necessary calculations:

- the electrophysiology trace was used to calculate the spiking rate $F$
- the updated speed for the robot, $V_r$, was calculated based on the choice of closed-loop controller
- the updated speed $V_r$ was sent to the robot via Bluetooth
- the current angular velocity of the robot $\omega_r$ was received via Bluetooth

In addition, the closed-loop software also synchronizes itself with the visual acquisition/display software using hardware triggering on the COM ports. This ensures that the images observed by the fly are synchronized with the control loop. The estimation of the spiking rate, $F$, and the implementation of the controller are described in the sections below.

**Spike Rate Estimation**

Sample electrophysiology traces of an H1 cell are shown in Fig 2.12. The signal-to-noise ratio of the electrophysiology recordings of the cell was crucial for the proper identification and separation of spikes from the background activity. The SNR for the recordings is defined as the ratio between the amplitude of the recorded H1 spikes and the amplitude or all other signals picked up by the electrode. Only recordings where the SNR $> 2$ were used for the closed-loop experiments. Once a good recording was obtained, the SNR of the signals typically remained stable for approximately 2.5 hours. Experiments were stopped if the SNR fell below its original level.

Spikes were separated from the background noise by using an amplitude threshold (shown in red in Fig 2.12). The threshold was applied to the electrophysiology signal to obtain the spike times. The value for the threshold was visually determined during recordings from the H1 cell under open-conditions.

After thresholding, the spikes were convolved with a causal, half-Gaussian filter
Figure 2.11: Diagnostic screen for the software processing routines required for the control loop. The screen allows for setting an appropriate threshold based on the amplitudes of the spikes in the H1 electrophysiology signals (here the signal from one H1 is mirrored in both the top-left and top-right panels). The corresponding instantaneous spike rates, \( F \), for the chosen thresholds are shown in bottom-left and bottom-right panels.

\( \sigma_{fr} = 50 \text{ms} \) to calculate an estimate of the instantaneous spiking rate. The choice of filter for estimation of the instantaneous spiking rate has an effect on the closed-loop performance of the system. A number of interrelated factors need to be taken into consideration when selecting a spiking rate estimation filter (i) its computational overhead should be small so that it is fast enough to operate within the closed-loop control delay (ii) the filter width \( \sigma_{fr} \) should be small to enable the detection of fast spike rate changes and (iii) \( \sigma_{fr} \) should be large enough to be able to calculate a smoothed estimate of the spiking rate. In a study involving the control of arm trajectories in monkeys using a brain-machine interface with visual feedback [Cunningham et al., 2009], it was shown that there was no significant performance gain observed in using complicated spiking rate estimation methods (e.g. adaptive
Figure 2.12: (a) Electrophysiology recording of an H1 cell shows a high signal to noise ratio. The high SNR allows spikes to be separate from the background activity using an amplitude threshold (dashed red line). Consistency in the shape of a single spike at the (b) start and (c) end of the experimental protocol shows the stability for the duration of the recording (approximately 45 – 60 mins).
smoothing, Bayesian methods) over simple Gaussian smoothing methods. Furthermore, the study found no significant difference in the closed-loop control of arm trajectories when the Gaussian width was increased from $\sigma_{fr} = 50\, \text{ms}$ to $150\, \text{ms}$. For the fly-robot interface, $\sigma_{fr} = 50\, \text{ms}$ was chosen to estimate the instantaneous spike rate.

It is essential that the choice of the spiking rate filter does not reduce the bandwidth of the neural signal below the bandwidth of the behavioural response being investigated. Warzecha and Egelhaaf [1996] proposed that the signal obtained by low-pass filtering (first order, $\tau_c = 750\, \text{ms}$) the differential activity of two H1 cells is highly correlated with the behavioural yaw torque response in *Calliphora*. Fig 2.13 shows the effects of two filters (i) causal half-Gaussian ($\sigma_{fr} = 50\, \text{ms}$) and (ii) low-pass filter ($\tau_c = 750\, \text{ms}$) on the bandwidth when applied to a white noise signal. The half-Gaussian filter has a drop-off at a higher frequency than the filter used to model the yaw torque of the fly making it more suitable for use as a spike rate estimator for the fly-robot interface.

![Firing Rate Filter Cutoff Comparison](image)

**Figure 2.13.** Gaussian white noise filtered by a first order low-pass filter with $\tau_c = 750\, \text{ms}$, and by a causal half-Gaussian kernel ($\sigma = 50\, \text{ms}$). The causal half-Gaussian kernel has a higher frequency cutoff $f_c$.

**Estimating the Robot Speed from the Spike Rate $F$**

In order to compute the updated speed of the robot, $V_r$, the spiking rate $F$ needs to be mapped onto an 8-bit value. This mapping is specific to the types of controller
being investigated and will be described in detail in the relevant chapters (Chapter 3 & 4). However, the general principle of the mapping remains the same. \( F \) is an estimate of the visual slip speed \((\omega_p - \omega_r)\) observed by the fly. When \( \omega_p = \omega_r \), there is no visual motion observed by the fly and the cell responds with its spontaneous spiking rate \( F_s \). However, when \( \omega_p > \omega_r \), the visual motion observed by the fly is in its preferred direction and the cell responds with a spiking rate between its spontaneous and its maximum rate \([F_s,F_{\text{max}}]\). Similarly, when \( \omega_p < \omega_r \), the visual motion is in the anti-preferred direction and the cell is inhibited. In this case, the H1 cell responds with a spiking rate between \([0,F_s]\). These response ranges of \( F \) can be mapped to an appropriate 8-bit compensation error range \( E \) for the robot. The compensation error can then be used to speed up/down the angular velocity of the robot depending on the amplitude and direction of the visual pattern motion.

### 2.2. Data Analysis Methods

All the data-sets were analyzed using custom written software programmed in Matlab (Version R2010a, Mathworks Inc.).

#### 2.2.1. Sampling of Turn-table (\( \omega_p \)) and Robot (\( \omega_r \)) Angular Velocities

The turn-table (\( \omega_p \)) and robot (\( \omega_r \)) angular velocities were sampled at 10 kHz and 20 Hz respectively. For the analysis in Chapters 3 and 4, \( \omega_p \) and \( \omega_r \) needed be compared to one another to quantify the performance of the closed-loop controllers. In order to facilitate the comparison, \( \omega_p \) and \( \omega_r \) were down and up sampled (cubic interpolation), respectively, to 100 Hz. The up-sampled robot angular velocities were filtered using a 3-point Gaussian kernel.

In Chapter 5, the visual stimulus velocity (\( \omega_p - \omega_r \)) was correlated to the H1 responses under closed-loop conditions. The limiting factor in sampling the stimulus velocity (\( \omega_p - \omega_r \)) at a higher rate was the low-sampling rate of the robot angular velocity (20 Hz). To circumvent this problem, the images captured by the cameras
were used to calculate a higher resolution signal of the stimulus velocity \((\omega_p - \omega_r)\) (cf. Reconstruction of Stimulus Velocity Using Camera Images) at 200 Hz.

### 2.2.2. Systems Identification Methods

To carry out system identification of the closed-loop fly-robot interface, step and frequency response characterizations were carried out.

#### Step Response Characterization

The step response characterization of two closed-loop controllers was carried out in Chapters 3 and 4. A step input \((\omega_p)\) was provided using the turn-table and the resulting robot angular velocity \((\omega_r)\) was measured.

\[
\omega_p = \begin{cases} 
144 \text{deg/s} & \text{if } t \geq t_i \\
0 & \text{if } t < t_i 
\end{cases}
\]

where \(t_i\) was the time at which the step input was provided.

The responses to a step input was parameterized by the variables illustrated in the Fig 2.14. The rise time was the time taken for the response signal to reach a specified percentage of the step’s steady state amplitude. It was calculated as the time taken for \(\omega_r\) to rise from \(0.05\bar{\omega}_p\) to \(0.95\bar{\omega}_p\), where \(\bar{\omega}_p\) is the step steady state value.

The settling time was the time taken for the response of the system to converge towards the amplitude of the step input. For the experiments carried out with different controllers, the response of the FRI never settled and therefore the settling time could not be calculated. Instead, the mean error between the step input and the robot response was calculated as \(\frac{1}{TFS} \sum |\omega_p - \omega_r|\), where \(T\) was the time over which the mean error was calculated while \(FS = 100\) Hz was the sampling rate for the \(\omega_p\) and \(\omega_r\) signals.

The percentage overshoot was the value in percent that the system’s response was
Figure 2.14.: The characteristic response of a control system to a step function. The response of the system to a step input can be parameterized by the rise time, percentage rise, settling time, percentage overshoot and undershoot. Image taken from explanation of the Matlab control toolbox.

higher than the step amplitude. This was calculated as \( \frac{\dot{\omega}_r - \omega_p}{\dot{\omega}_p} \), where \( \dot{\omega}_r \) was the peak of the robot response as it initially exceeded the step input.

Similarly, the percentage undershoot was the percentage amount that the system response could undershoot beyond it’s initial value. Under closed-loop conditions, the robot (\( \omega_r \)) and turn-table (\( \omega_p \)) were constrained to rotate in the clockwise and counter-clockwise directions respectively. For an undershoot to occur at the onset of a step input \( \omega_p \), the robot would have to rotate counter-clockwise such that \( (|\omega_r| > |\omega_p|) \). As this was not possible due to the restrictions in the robot’s rotation direction, no undershoot was observed for any of the experiments. To the extent of our knowledge, it is not possible to conclude from previous behavioural experiments whether or not flies exhibit undershoot during an optomotor task.
Frequency Response Characterization

The frequency response characterization was carried out for the two closed-loop controllers in Chapters 3 and 4 and the stimulus-response properties of the H1 cell in Chapter 5. To calculate the frequency response, sinusoidal functions were used to modulate the angular velocity of the turn-table, $\omega_p$, and the corresponding robot angular velocity, $\omega_r$, was measured. The sinusoidal velocity modulations, $\omega_p$, were superimposed onto a constant rotation of the turn-table in the counter-clockwise direction in order to always stimulate the H1 cell along its preferred direction:

$$\omega_p = 72 \cdot \sin(2\pi f_i t) + 72$$

where, $f_i$ is the input frequency (Hz).

The fly-robot response was probed over a range of frequencies $f_i = [f_1, f_2 \ldots f_n]$:

$$U(t) = \begin{cases} 72 \cdot \sin(2\pi f_1 t) + 72 \\ 72 \cdot \sin(2\pi f_2 t) + 72 \\ \vdots \\ 72 \cdot \sin(2\pi f_n t) + 72 \end{cases}$$

and the corresponding robot responses $\omega_r$ were observed.

$$Y(t) = \begin{cases} G\{72 \cdot \sin(2\pi f_1 t) + 72\} \\ G\{72 \cdot \sin(2\pi f_2 t) + 72\} \\ \vdots \\ G\{72 \cdot \sin(2\pi f_n t) + 72\} \end{cases}$$

where G is the unknown closed-loop transfer function.

Both $U(t)$ and $Y(t)$ were converted into the Fourier domain and the amplitude and
phase components obtained at the input frequencies $f_i = [f_1, f_2 \ldots f_n]$:

$$
\begin{align*}
U_{amp} &= \{A_{U_1}, A_{U_2}, \ldots, A_{U_n}\} \\
Y_{amp} &= \{A_{Y_1}, A_{Y_2}, \ldots, A_{Y_n}\} \\
U_{\phi} &= \{\phi_{U_1}, \phi_{U_2}, \ldots, \phi_{U_n}\} \\
Y_{\phi} &= \{\phi_{Y_1}, \phi_{Y_2}, \ldots, \phi_{Y_n}\}
\end{align*}
$$

The amplitudes, $(Y_{amp}, U_{amp})$, and phases, $(Y_{\phi}, U_{\phi})$, were calculated using an FFT with a Hanning window function. The magnitude, $20\log_{10}\left(\frac{Y_{amp}}{U_{amp}}\right)$ and phase, $(Y_{\phi} - U_{\phi})$ components of the closed-loop frequency response were calculated over the range of input frequencies $f_i = [0.03, 0.1, 0.3, 0.6, 1.0, 3.0]$.

### 2.2.3. Estimation of Robot Transfer Function

The Bode gain and phase measurements of the rotation of the robot (shown in Fig 2.4) were used to estimate the transfer function, $G(s)$, for the input-output relationship between $V_r$ and $\omega_r$. The mean response for both the gain and phase were estimated from the individual measurements over the frequency range $0.03 - 3$ Hz. An iterative search algorithm (Output-Error model command OE, Matlab’s System Identification Toolbox, version R2010a, Mathworks Inc.) was used to fit the parameters to three models: M1 (1-zero,2-poles), M2 (1-zero,3-poles), M3 (2-zero,3-poles). The best fit for the robot frequency response was obtained for M3 (85.4)

$$
G(s) = \frac{1.73}{s^2 + 1.87s + 0.86}
$$

### 2.2.4. Reconstruction of Stimulus Velocity Using Camera Images

The visual stimulus velocities observed by the fly under closed-loop conditions can be calculated as the difference in angular velocities of the robot and the turn-table
\(\omega_p - \omega_r\). The limiting factor in estimating the stimulus velocity is the sampling rate of the robot angular velocity \(\omega_r\) which was 20 Hz. In order to be able to correlate the closed-loop stimulus velocity with the spike rate activity of the H1 cell, the relative velocity signal \(\omega_p - \omega_r\) needs to be sufficiently up-sampled. Alternatively, the visual slip-speed can be estimated from the images captured by the cameras on the robot. These images were the instantaneous visual input to the blowfly over time and were sampled at a much higher rate of \(\approx 200\) Hz. Motion vision algorithms were used to extract the horizontal visual slip-speed from the camera images as described below.

**Motion Information in Optic Flow Fields**

In the experimental system, the relative motion between the turn-table and robot is captured by the high-speed cameras. The optic flow fields (cf. Processing of Visual Motion by LPTCs, Chapter 1) can be calculated from the images to calculate the velocity of the vertically oriented grating pattern. As both the turn-table and robot are both constrained to rotate only along the horizontal plane, only the horizontal rotation component of the pattern motion needs to be estimated from the optic flow fields. This horizontal or yaw rotation corresponds to the self-motion component the receptive field of the H1 is tuned to detect (Fig 1.6). The pyramidal Lucas-Kanade algorithm [Bouguet, 2000] (cf. Appendix A1) was used to estimate the horizontal optic flow from the camera images.

**Estimation of Stimulus Velocity using the Pyramidal Lucas-Kanade Method**

The first step was to determine the parameters that best suit the pyramidal Lucas-Kanade method given the set of images generated by the cameras. The pyramid method has two sets of parameters, the window size, defined in pixels, and the number of pyramids used. Increasing the window size gives a better estimate over a given region, but reduces the resolution obtained, while increasing the number of pyramids allows for estimating larger pattern motion at the expense of losing resolution at lower pattern image velocities. Different window size (5,15,25) and number of pyramids (0,1,3,5) were used to calculate optic flow for motion of known
pattern velocity. The results are shown in Fig 2.15 below. The performance of the pyramid method seems to depend more on the window size rather than the number of pyramid levels used. For the range of values shown, the performance is roughly similar, with greater accuracy achieved for larger window sizes. The errors in calculation became very high when increasing the number of pyramids (not shown - level 7+).

The best performance of the pyramidal Lucas-Kanade method is achieved with no pyramid levels and a window size of 25x25 pixels (Fig 2.15). It can be seen from Fig 2.16a that the output of the pyramidal method, $V_o$, (no pyramid levels, window size 25x25 pixels) scales linearly with the true stimulus velocity ($\omega_o$):

$$V_o = 0.0995 \cdot \omega_o - 0.3595$$

The standard deviation for the range of stimulus velocities observed under closed-loop conditions ($< 150 \text{ deg/s}$) is also very low ($< 1 \text{ deg/s}$). Additionally, the mean latency between the stimulus velocity estimated from the turn-table and robot signals ($\omega_p - \omega_r$) and the stimulus velocity estimated from the camera images was
1.4 ± 0.77 ms (mean±std), which was well within the sampling rate for the camera images ($dt = 5$ ms).

Figure 2.16: (a) Linear relationship between the true stimulus velocity, $\omega_o$, and the output of the pyramidal Lucas-Kanade method, $V_o$ (no pyramid levels, window size 25x25 pixels) (b) standard deviations in estimating the true stimulus velocity $\omega_o$ are very small (< 1.4 degs/sec)

2.3. Summary

The fly-robot interface (FRI) presented in this chapter fulfills the four design requirements for an experimental system needed to investigate optomotor control principles in the fly (cf. Limitations of Existing Experimental Systems, Chapter 1). It is inspired by the virtual flight simulator experimental setup used by Warzecha and Egelhaaf [1996]. The FRI allows for the simultaneous measurements of both the physical torque (relative angular velocity between the turn-table and the robot) and the visually-mediated neural activity (H1 LPTC) generated during a closed-loop visual stabilization task along 1-DoF. The neural activity is used to control the angular velocity of a mobile robot which provides the experimental system with real-world physical interaction. Additionally, the software interface was designed such that different control laws could be used to close the loop between the neural activity and the robot response. Finally, angular velocity inputs with step and sinusoidal profiles can be used to introduce external perturbations within the
closed-loop system which allows for the subsequent analysis to be carried out using step and frequency characterization methods from control theory.
3. Dynamics of closed-loop visuo-motor stabilization under proportional control

In the previous chapter, an experimental platform consisting of a fly-robot interface (FRI) was described. In addition, the dynamics of its components (robot and turntable), were characterized. By using the activity of an identified visual interneuron, the H1 cell, to control the angular velocity of the robot, the fly could stabilize its gaze by compensating for and stabilizing the visual motion observed under closed-loop conditions.

In this chapter, a linear feedback proportional controller was used to close the loop between the activity of the H1 cell and the rotational speed of the robot. By constraining the FRI to a visual stabilization task along 1-DoF (horizontal yaw rotation), the neural activity of the cell was recorded while monitoring the behavioural performance (relative angular velocities between the turn-table and the robot) of the FRI in minimizing retinal slip-speed (pattern motion speed). The step and frequency responses of the FRI with the proportional controller were probed using a square-wave grating pattern. No specific value of the manually adjusted closed-loop controller gain was able to perform visual stabilization optimally over the frequency range tested. The results with the proportional controller predict that the best strategy for the fly would be to continuously adapt the closed-loop controller gain depending on the angular velocity and acceleration of the observed visual slip-speed.
3.1. Closing the loop for the fly-robot interface

3.1.1. Fly-robot interface for optomotor control

The fly-robot interface was inspired from the classic fly optomotor experiments where the visually induced yaw torque generated by the fly was used to minimize image motion on a computer CRT monitor [Reichardt and Wenking, 1969, Gotz 1962]. In the experimental setup, the neural activity of the H1 cell was used (in place of the yaw torque) to control the angular rotation of the robot. The visual display (Fig. 3.1), consisted of a cylindrical drum, the walls of which were lined with vertically oriented black and white stripes (spatial wavelength $\lambda_{sp} = 11^\circ$). The robot was placed on a turn-table in the centre of the drum. Both turn-table and robot movements were limited rotations around the vertical yaw axis at angular velocities $\omega_p$ and $\omega_r$ respectively. Visual image motion generated as a result of the relative motion between the turn-table and the robot ($\omega_p - \omega_r$) were captured by two high-speed video cameras mounted on the robot (at 200 fps) and displayed on two high-speed CRT monitors placed in front of an immobilized fly. The visual motion presented to the fly caused spiking activity in the H1 cell [Krapp et al., 2001], which was recorded and the signals used within a linear feedback control framework to drive the two motors on the robot thus closing the optomotor loop.

3.1.2. Proportional controller as a static gain feedback controller

To close the loop for the fly-robot interface, a negative feedback controller was used to minimize the visual motion observed by the fly. Proportional-integral-derivative (PID) controllers are a set of generic linear controllers that are used to minimize the closed-loop error, as calculated by the difference between the system’s desired set point and the process output Figure 3.2. The equation for a generic PID controller is given as:
Figure 3.1.: Optomotor control using the fly-robot interface. The robot was placed on a
turn-table within a cylindrical arena whose walls are lined with a vertically
oriented grating (spatial wavelength $\lambda_{sp} = 11^\circ$, pattern contrast). The motion
of the robot and turn-table were limited to yaw rotations. Relative motion
between the robot and turn-table was captured at 200 fps via two high speed
cameras mounted on the robot. The robot rotation compensated for the visual
motion as a result of the rotation of the turn-table.

Figure 3.2.: Block diagram of a generic PID controller. The controller calculates the
input to the process block based on the instantaneous closed-loop error and
the constant gains associated with the proportional ($K_p$), integrative ($K_i$) and
derivative stages ($K_d$).

\[
PID_{output} = K_p \cdot e(t) + K_i \cdot \int e(\tau) d\tau + K_d \cdot \frac{d[e(t)]}{dt} \tag{3.1}
\]

where $e(t) =$ set point - process output is the error signal to the PID controller,
and $K_p, K_i$ and $K_d$ are the gains for the proportional, integral and derivative stages
respectively.
Eq 3.1 shows that the PID output is the sum of the parallel proportional, integral and derivative stages. The proportional stage simply scales in proportional to the error \( e(t) \) using a gain \( K_p \). The integral stage contributes to the overall sum by integrating the error over a fixed time period and scaling the resulting term by the gain \( K_i \). Finally, the derivative stage scales the derivative of the error \( e(t) \) by the gain \( K_d \). The values of all three stages are summed to calculate the PID output. The closed-loop gains \( K_p \), \( K_i \) and \( K_d \) for the PID controller are either tuned manually or by means of automated methods (review: O’Dwyer [2006]).

The simplest form of the generic PID form is the proportional controller. The proportional controller disregards the outputs of the integral and derivate stages \((K_i = K_d = 0)\) and only estimates the controller output based on the proportional stage with gain \( K_p \). To my knowledge, all behavioural studies so far on fly opto-motor responses in a closed-loop flight simulator have used proportional feedback control with a manually adjusted gain \( K_p \) (e.g. see: using yaw torque [Mayer 1989] Warzecha and Egelhaaf 1996 Wolf and Heisenberg 1990], using wing-beat analysis [Chow and Frye 2008 Graetzel et al.] 2010 2008 Theobald et al. 2009], using front-legs [Reinhard et al. 1992]).

3.1.3. Closed-loop proportional control

The block diagram for the closed-loop fly-robot interface is shown in Fig 4.2b. As mentioned earlier, the experimental system was setup such that the relative motion (slip speed) between the turn-table and the robot caused spiking activity, \( F \), in the H1 cell being recorded from. These H1 responses were used by the proportional controller to update the angular velocity of the robot, \( \omega_r \), in order to compensate for the external visual perturbations as a result of the turn-table’s rotation.

The H1 cell increases its spike rate upon visual motion from back-to-front (preferred direction - PD) and is inhibited by front-to-back motion (null direction - ND). The response of the cell was measured as a spike rate, \( F \), which was a function of the visual slip speed, \( \omega_p - \omega_r \). When there was no visual motion (i.e. the pattern was stationary), the cell responded with a spontaneous spiking rate, \( F_s \). When stimulated in its PD, the cell responded with a maximum spiking rate \( F_{\text{max}} \).
Figure 3.3.: Block diagram of closed-loop FRI using a proportional controller. The relative motion (slip speed) between the turn-table and the robot $\omega_p - \omega_r$ caused spiking in the H1 cell at an instantaneous rate $F$. The H1 responses (spike rate $F$) were used by a real-time controller to compensate for the visual displacement by driving the robot in the opposite direction to the turn-table. The converter maps $F$ to a compensation error $E$ based on sigmoid function. $E$ was then used to update the robot speed $V_r$.

between the contrast frequency range of $2 - 4$ Hz [Warzecha et al., 1999]. Prior to the actual closed-loop experiments, both $F_s$ (Mean ± SE : 19.67 ± 2.3) and $F_{max}$ (Mean ± SE : 78 ± 4.27) were estimated in open-loop for each fly using 3 repeats of 5 second stimulation with no pattern motion and motion in the PD (contrast frequency - 3 Hz), respectively. Estimates of the maximum spiking rate $F_{max}$ varied when measured across different flies (N=7) (see Fig 3.4). This inter specific variability is likely to reflect the natural variations as observed across different flies.

The H1 spike rate, $F$, was then mapped onto a compensation error $E$. Two considerations were taken into account at this point. Firstly the spike rate, $F$, of the cell was the most sensitive around the spontaneous rate, $F_s$, with any large deviation from $F_s$ causing a rotation of the robot. In order to counter this, a sigmoid function was used for the mapping of $F$ onto $E$ as shown in Fig. 3.5. A cosine function over the range $[-1, 1]$ was mapped independently on to the ranges $[0, F_s)$ and $(F_s, F_{max})$ in order to obtain a sigmoid relationship between $F$ and $E$ in the null and preferred directions respectively. Secondly, the robot speed was controlled by an 8-bit value $V_r$ which set the limits of the overall dynamic range for the actuator. As a result $E$ was mapped within the 8-bit range described by $-E_{max} \leq E \leq E_{max}$. Additionally, since the sensitivity to visual motion for the H1-cell is very low in the null direction, decreasing the error, $E$, in proportion to the spike rate $F$ in the null direction would lead to prominent oscillations in the robots rotation response.
Figure 3.4.: Maximum spiking rates $F_{\text{max}}$ estimates for the H1 cell ($N=7$ flies) over a period of 5 s with 3 repeats. The measurements of $F_{\text{max}}$ across different flies were highly variable.

As a result, the speed of the robot $V_r$ was constrained to only decrease by 25% of its previous value (25% of value in previous control loop iteration: $\frac{1}{4}[V_r(t) - \hat{V}_r]$) for visual motion in the null direction. Taking all these factors into account, the mapping $F \rightarrow E$ was defined by:

$$
E = \begin{cases} 
- \frac{E_{\text{max}}}{2} \{\cos (2\pi \phi) + 1\} \left\{\frac{1}{4} (V_r(t) - \hat{V}_r)\right\} & \text{for } F < F_s, \\
0 & \text{for } F = F_s, \\
\frac{E_{\text{max}}}{2} \{\cos (2\pi \phi) + 1\} & \text{for } F > F_s,
\end{cases}
$$

where, $\phi = -\frac{1}{2} \left(\frac{F}{F_s}\right)$

Here $\hat{V}_r$ is the speed offset that defines the value where the robot first starts to rotate from rest.

The speed of the robot was updated using a proportional controller with gain $K_p$.
Figure 3.5.: Sigmoid function used to map $F$ to $E$ for motion in the PD and ND. It has a higher gradient in the range $F < F_s$ to account for the increased sensitivity to visual motion in the ND.

by:

$$V_r(t + 1) = K_p \cdot E + V_r(t),$$

where the angular velocity of the robot is determined by:

$$\omega_r = G(s) \cdot V_r,$$

and where $G(s)$ is the transfer function (cf Section 2.2.3) of the robot and is given as:

$$G(s) = \frac{1.73}{s^2 + 1.87s + 0.86}$$

### 3.1.4. Closed-loop Experiments

The step and frequency responses of the fly-robot interface under closed-loop conditions were characterized for the proportional controller with $K_p = [0.01, 0.1, 0.5, 1.0]$. The responses were obtained for $N = 5$ flies for $K_p = [0.01, 0.1, 0.5]$ and $N = 7$ flies for $K_p = 1.0$. The step response stimulus was delivered by the turn-table as:

$$\omega_p = \begin{cases} 
0 & \text{for } t < 2.5 \text{ s,} \\
144 \text{ deg/s} & \text{for } t \geq 2.5 \text{ s,}
\end{cases}$$

Similarly, the closed-loop frequency response was characterized over the range $0.03 \leq f_i \leq 3.0$ Hz. A sine-wave with a DC-offset was used so that the H1 cell
Figure 3.6: Mean step response of the fly-robot interface with the proportional controller. The turn-table moved by a step-shaped input angular velocity function with a DC value of $\omega_p = 144$ deg/s. Mean and standard deviation of the robot responses are shown for $K_p = 0.01, 0.1, 0.5, 1.0$.

was stimulated mostly in its preferred direction over an input range that spans $0 \leq \omega_p \leq 144$ deg/s:

$$\omega_p = 72 [\sin(2\pi ft) + 1]$$

### 3.2. Step Response Characterization

The step responses of the closed-loop proportional controller for $K_p = 0.01, 0.1, 0.5, 1.0$ are shown in Fig. 3.6. To quantify the differences of the step responses for different $K_p$ values, the rise time, percentage overshoot and mean error were calcu-
Figure 3.7: Step response characterization for the proportional controller (a) Rise times decreased with increasing $K_p$ (b) Percentage overshoot increased with increasing $K_p$ (calculated as $\hat{\omega}_r - \omega_p$ where $\hat{\omega}_r$ was the peak of the robot response as it initially exceeded the step input) (c) Steady-state error, as measured with a step input $(\frac{1}{T} \sum |\omega_p - \omega_r|$, where $T$ was the time over which error was calculated and $S$ was the sampling rate of turn-table and robot signals. Due to the distribution of the signal $\omega_p - \omega_r$, the values of $T$ were different when estimating errors in the PD and ND. An asymmetry exists in the way the H1 cell estimates motion in the PD and ND. This is reflected in the mean errors. (d) Mean power spectra for the step responses $\omega_r$ ($K_p = 0.01, 0.1, 0.5, 1.0$).

labeled (see Fig. 3.7). The mean error (in both preferred and anti-preferred directions) is shown in Fig. 3.7c. Possibly due to the variability in neuronal spiking as well as the PD-ND asymmetry in H1 motion estimation, the response of the system did
not settle for increasing values of $K_p$. Therefore, the settling time could not be calculated.

At small values for the controller gain, $K_p = 0.01$, the rise time for the FRI initial response was markedly longer compared to cases with large $K_p$ (Fig. 3.6a). Increasing $K_p$ to 0.1 decreased the mean rise times and the mean response $\omega_r$ appeared to settle around the value of the step input (Fig. 3.6b). While the mean response settled, individual responses did not due to the variability in H1 cell responses. Increasing $K_p$ further to 0.5 resulted in shorter rise times but a clear overshoot emerged (Fig. 3.6c). Increasing $K_p$ further beyond this point did not result in further reduction of rise times which was possibly due to the limited dynamics of the robot (Fig. 3.6d).

For $K_p = 1.0$, the mean response $\omega_r$ oscillated at a fixed amplitude around the step input. The power spectra of the slip-speed observed by the fly for different controller gains $K_p$ (Fig. 3.7d) shows increased power at 1 Hz for increasing $K_p$. This indicates that 1 Hz is the natural frequency $f_n$ [Ogata, 1997] of the closed-loop FRI that causes oscillations in the response which have an impact on the accuracy of the steady-state error measurements for the step input.

Although increasing $K_p$ shortened the rise times (Fig. 3.7a) of the FRI, the increased oscillations (Fig. 3.7b) reduced its ability to continuously compensate for the constant input $\omega_p$. Also, an increased $K_p$ had an asymmetric effect on the mean error of the respective motion in the H1 cell’s preferred and null directions. A conventional proportional controller assumes the sensor to provide a symmetric error estimation around the desired set point. For the FRI, the sensor measuring slip-speed error was the H1 cell which has a strong asymmetry in its sensitivity to motion in the PD and ND. This asymmetry is reflected in the mean error observed for the FRI step response (Fig. 3.7c). The asymmetry measured as a function of the mean error in the PD and ND became larger for increasing $K_p$. It should be noted that this is despite the compensation error $E$ resulting from motion in the ND being limited to 25% of that in the PD. While the asymmetric response to PD and ND motions seems to limit the accuracy at which a steady-state perturbation can be compensated for, it has been proposed to support closed-loop object fixation behaviour [Wolf and Heisenberg, 1979].
To summarize the effect that an increased value of $K_p$ had on the dynamics of the step response: higher values of $K_p$ decreased the rise times of the mean response but increased the amplitude of oscillations around the value of the constant input at the natural frequency of the system.

### 3.3. Frequency Response Characterization

The frequency response of the system was used to probe the effects of the proportional controller on the responses to visual perturbations of different angular velocities and accelerations. Sinusoidal inputs with input frequency $f_i$ ranging over $0.03 \leq f_i \leq 3.0$ Hz were used to characterize the system’s behaviour for the different controller gains $K_p$.

Fig. 3.8 shows two sample traces of the turn-table and robot responses for a sinusoidal input ($f_i = 0.1$ Hz) and a proportional controller gain $K_p = 0.1$ & 0.5. For $K_p = 0.1$, the robot response followed the turn-table response closely, therefore minimizing the visual-slip speed observed by the fly. However, for the same input frequency $f_i$, increasing $K_p$ to 0.5 decreased the robot’s ability to accurately track the turn-table angular velocity, increasing the observed visual slip-speed. Increasing the controller gain also increased the oscillations observed in the robot response, a result consistent with the dynamics observed during the step response characterization described in the previous section. The effect of increased oscillations in the robot response as a result of a high controller gain $K_p$ can be observed as an increase in the power at 1 Hz. The oscillations observed in the response of the FRI with sinusoidal inputs are at the same frequency (1 Hz) as observed with step inputs (see Fig. 3.7d). This indicates that 1 Hz is indeed the natural frequency of the closed-loop FRI.

Fig. 3.9 shows the bode plot of the closed loop system over the input frequency range $0.03 \leq f_i \leq 3.0$ Hz. The gain plot of the responses for $K_p = 0.01$ indicates a very low system gain with the responses dying out very quickly for higher input frequencies. The system gain is high enough for lower frequencies, but dropped for $f_i \geq 0.3$ Hz. For $K_p = 0.1$ the performance was slightly improved. At this
Figure 3.8.: Sample turn-table vs robot responses for sinusoidal inputs. (a-b) Sample turn-table and robot responses angular velocities for a sinusoidal input \( f_i = 0.1 \) Hz and proportional controller gain \( K_p = 0.1 \) & 0.5. For \( K_p = 0.1 \), the robot followed the turn-table response well and minimized the visual slip-speed observed by the fly. Increasing \( K_p = 0.5 \) caused oscillations in the robot response, indicating a high controller gain. (c) The effect of increasing \( K_p \) on the oscillations are seen as an increased power in the spectrum of the robot response for \( K_p = 0.5 \) at 1 Hz.

\( K_p \) value, a peak in gain emerged at 1 Hz, which earlier has been identified as the natural frequency of the closed-loop system. The performance at \( K_p = 0.5 \) was roughly equivalent to that for \( K_p = 0.1 \), though the increase in \( K_p \) accounts for the increased system gain at input frequency \( f_i = 0.3 \) Hz. At \( K_p = 1.0 \), the system gain was approximately constant over the input frequency range \( 0.03 \leq \)
When compared to the smaller controller gains $K_p = 0.1$ and $0.5$, the system gains for $K_p = 1.0$ were smaller for lower ($0.03 \leq f_i \leq 0.3$) and larger for higher ($0.6 \leq f_i \leq 1.0$) input frequencies. This is because, although the high gain allows better rise times, it does so at the cost of increased oscillations. As a result, tracking performance for the turn-table angular velocity profile at lower input frequencies is reduced. Peak performance of the system gain was observed at the natural frequency of the system i.e. 1 Hz. In general, when increasing the controller gain $K_p$, the performance of the closed-loop FRI depended on the stimulus frequency.

Figure 3.9.: Bode system and phase plots of the frequency response of the closed-loop system. The responses were probed over the frequency range $0.03 \leq f_i \leq 3$ Hz. Different colours represent measurements with different controller gains.
A small controller gain, $K_p = 0.01$, yielded poor performance across all frequencies tested. Increasing the controller gain $K_p$, improved the system gain at low input frequencies $f_i$ as long as $K_p$ was within a certain range ($0.1 \leq K_p \leq 0.5$). However, $K_p$ in this range also resulted in the decrease of the system gain at higher input frequencies ($f_i = 0.6$ Hz). A large $K_p$ also increased oscillations around the natural frequency, $f_n$, of the closed-loop system. Increasing the gain even further caused an approximately constant system gain for all $f_i \leq 1$ Hz. Similarly, for the phase, a lower $K_p$ lead to the robot responding slower to any visual input and spike rate changes of the H1 cell. This caused increased phase delays between turn-table and robot movements. As can be seen in the phase plot, larger $K_p$ lead to a smaller phase lag between the input and output at higher input frequencies, $f_i$. For very high input frequencies, $f_i = 3$ Hz, the system gain for all controller gains, $K_p$, was very low. This was due to the limitations imposed by the robot not being able to rotate at such a high frequency.

### 3.3.1. Performance Index

One way of assessing the performance of the FRI with the proportional controller is to use optimal control theory. The task of stabilizing the image motion under closed-loop conditions can be formally defined as a minimization problem. Specifically, the problem can be defined as a variant of linear quadratic optimal controller ([Todorov, 2006](#)). Intuitively, a cost function needs to be minimized which takes into account both the performance of the FRI, i.e. how well it is able to keep image velocities at 0 deg/s, and the effort required for control, i.e. the total energy expended by the H1-cell in producing action potentials. Therefore, the performance cost function, $J_i$, was defined to assess the efficiency of the controller in stabilizing the visual motion observed by the fly for different controller gains $K_p$:

$$J_i = \frac{1}{T_i} \left( \alpha_F \cdot J^i_{in} + \alpha_{slip} \cdot J^i_{out} \right)$$  

(3.2)

where $T_i$ is the total time of the closed-loop measurements, $\alpha_F$ and $\alpha_{slip}$ are the associated input and output weights and $J^i_{in}$ and $J^i_{out}$ are the energy of the spike rate (input) and the slip-speed (output) signals respectively measured at the input.
Figure 3.10: Proposed performance index, $J_i$, calculated for three conditions where (a) neural energy requirements dominate those of the actuator ($\alpha_F = 0.1, \alpha_{slip} = 0.9$) (b) actuator energy requirements dominate those of the neural response ($\alpha_F = 0.9, \alpha_{slip} = 0.1$) (c) neural and motor energy requirements are balanced ($\alpha_F = 0.5, \alpha_{slip} = 0.5$).

frequency $f_i$. 

$$J_{in}^i = \int_0^\infty F_i^2 dt$$  \hspace{1cm} (3.3)
\[ J_{\text{out}} = \int_0^\infty (\omega'_p - \omega'_r)^2 \, dt \]  

(3.4)

\( \omega'_p - \omega'_r \) in Eq. 4.4 corresponds to the visual slip-speed observed by the fly under closed-loop conditions and indicates the compensation error. The larger it is, the worse the compensation by the controller. \( F_i \) in Eq. 3.3 indicates the energy spent by the H1 cell. An optimal controller therefore should minimize \( J_i \) over the desired operating range \( f_i \), by achieving the smaller error \((\omega'_p - \omega'_r)\) with smaller input energy. \( J_i \) at \( f_i = 3 \) Hz was disregarded since the system gain for the controller was very low at this input frequency.

Different weights can be assigned to the input \( (J_i') \) and the output \( (J_{\text{out}}) \) to assess their relative contribution to the overall performance. The overall performance \( J_i \) can be tested under three different configurations (i) there is less penalty in using a lot of energy to achieve slip-speed reduction \([\alpha_{F} \alpha_{\text{slip}} \text{ is low}]\) (ii) there is a strong constraint on the energy that can be used by the neural system to achieve slip-speed reduction \([\alpha_{F} \alpha_{\text{slip}} \text{ is large}]\) (iii) the energy constraint and the requirement to achieve good output are balanced \([\alpha_{F} \alpha_{\text{slip}} = 1]\). The effect of altering \( \alpha_F \) and \( \alpha_{\text{slip}} \) on the overall performance \( J_i \) is shown in Fig. 3.10.

In case the neural energy requirements dominate over those of the closed-loop error requirement (Fig. 3.10a), increasing \( K_p \) increased \( J_{\text{in}} \) and therefore decreased the overall performance \( J_i \). This did not hold true for \( K_p = 0.01 \) where the FRI already nearly failed to track the input angular velocity profile as a result of a very small controller gain. There was no qualitative difference between (ii) and (iii) except that the differences in the performance index \( J_i \) for different \( K_p \) were more pronounced (Fig. 3.10c & 3.10b).

In both (ii) and (iii), there was no specific value of \( K_p \) that provided optimal control at all input frequencies \( f_i \). Instead the FRI performance at an input frequency, \( f_i \), was dependent on the controller gain, \( K_p \). For \( 0.03 \leq f_i \leq 0.1 \), \( K_p = 0.1 \) gave the best performance. For \( f_i = 0.3 \), the best performance was achieved for \( K_p = 0.5 \) while for \( f_i = 0.6 \), the optimal gain was \( K_p = 0.1 \). For \( f_i = 1.0 \), the best choice for controller gain was again \( K_p = 0.5 \). While the performance curves for \( K_p = 0.01 \)
and $K_p = 1.0$ are very similar, the underlying mechanisms for control were very different. For $K_p = 0.01$, the response time for the FRI was high, so there was a large build up of error leading to a decrease in the performance index $J_i$. For $K_p = 1.0$, the response time was fast but the system oscillated around the input angular velocity, resulting in a low performance index. What is also observed is that for $0.03 \leq f_i \leq 0.1$, there was a large difference between the performance of the FRI for $K_p = 0.1, 0.5$ compared to $K_p = 0.01, 1.0$. Again, this can be explained in terms of the oscillations observed in the FRI response for increasing values of $K_p$. Smaller gains were best suited for input frequencies $0.03 \leq f_i \leq 0.1$ which have low angular accelerations. As the angular acceleration of the input signal, $\omega_p$, increased, the FRI with low gain was unable to follow the input stimuli because of slower response times. This implies that for different input frequencies $f_i$, the performance index of the system would be optimized by a different controller gain $K_p$. This suggests that an optimal controller for such a system would be one which automatically adjusts its controller gain based on the prevailing input angular velocity and acceleration of the visual perturbation.

### 3.4. Discussion

The fly–robot interface presented in this chapter allows for the characterization of the step and frequency response dynamics with a proportional controller. The analysis differs from previous closed-loop neural [Warzecha and Egelhaaf, 1996] and behavioural studies [Mayer, 1989; Wolf and Heisenberg, 1990] in that the dynamics of individual responses of the FRI were characterized and the analysis was not just limited to averages over trials. Recent studies in *Drosophila* have characterized the dynamics of visuo-motor control in both open and closed-loop at the behavioural level [Graetzel et al., 2010; Rohrseitz and Fry, 2010]. With the FRI, optomotor control strategies in *Calliphora* can be investigated by correlating the neural activity of the H1-cell with the behavioural performance of the robot.

For studying sensorimotor control within the framework of optimal closed-loop control [Todorov, 2004] proposed two requirements (i) the specification of the family of control laws which are used to accomplish a given task and (ii) to formulate
appropriate measures which quantify the performance of the task. The characterization of the closed-loop system using inputs with step and sinusoidal profiles indicate first and higher order system dynamics as well as the gain and phase relationship between the input and output of the system. [Tin and Poon] [2005] also observe that measures of performance that include stability criteria, i.e. gain and phase differences between the system input and output, are not always included in the study of sensorimotor control. As a result the step and frequency response functions of the FRI can serve as both a systems characterization as well as measures of performance for the optomotor task being investigated.

The step response of the FRI revealed typical characteristics of a proportional controller. Increasing the controller gain $K_p$ shortens the rise times (Fig. 3.7a). The rise times however cannot be shortened beyond the limits set by the dynamical properties of the actuators, in this case the robot. For the fly, a fast rise would be advantageous as it would reduce the delay in a behavioural response to the rapid onset of a visual stimulus. A faster response, however, comes at the cost of increased overshoot (Fig. 3.7b) and oscillations (Fig. 3.6d), both of which are undesirable in a task that involves the stabilization against visual motion. Increased oscillations in the step response may be as a result of a high controller gain $K_p$. In previous behavioural studies involving closed-loop optomotor control in *Drosophilla*, pronounced yaw torque fluctuations were observed in individual responses [Mayer 1989, Warzecha and Egelhaaf 1996, Wolf and Heisenberg 1990]. In these experiments, a proportional controller was used for closed-loop feedback and the controller gain was arbitrarily chosen to provide acceptable mean error in the responses. The oscillations observed in these optomotor experiments may in part be attributed to a high controller gain, as the work presented in this chapter suggests. Comparisons between experiments using yaw torque or neural responses for feedback to control an actuator are reasonable since in a previous study the torque response and the differential response of the two H1 cells in the blowfly were shown to be correlated [Warzecha and Egelhaaf 1996].

A limitation of the FRI is that the activity of only one H1-cell is used for controlling the angular rotation of the robot. The fly however has two H1-cells (c.f. 1.3.4, Chapter 1), one in each visual hemisphere. During yaw rotations in a given
direction, one of the H1-cell’s is always stimulated by motion in its PD while at the same time the other is inhibited due to ND motion [Krapp et al., 2001]. Kern and Egelhaaf [2000] occluded one eye in *Lucilia* and measured the turning responses in both freely flying and walking flies inside a visual arena. The authors concluded that it was hard to tell from the turning responses that the fly had been limited to the use of monocular vision and that while the flies exhibited a slight turning preference towards the stimulated eye, no such asymmetry could be observed in individual responses.

The effect of high controller gain on increased slip-speed while using two H1 cells for closed-loop optomotor control has been shown in *Calliphora* [Warzecha and Egelhaaf, 1996]. In that study, a step input was used and the mean slip-speed error was calculated for different controller gains. By initially starting with a low controller gain, the mean slip-speed error was shown to initially decrease for increasing controller gain. However, as the controller gain was further increased, the mean slip-speed error was increased. A proportional controller was used in the study and the increased slip-speed error observed is consistent with the control oscillations due to a high controller gain.

Slip-speed oscillations as a result of a proportional controller with high gain have also been shown in an optomotor modeling study in *Calliphora* [Lindemann et al., 2008]. In the study, the differential activity of two complementary visual interneurons (the left and right HSE cells) was used for the optomotor stabilization of visual perturbations observed by a virtual fly in a closed-loop flight simulator. Oscillations around the constant input were observed for increasing values of the controller gain. While using two H1’s for controlling the robot would no doubt improve the performance in tracking a step input, the oscillations observed with the FRI are entirely consistent with existing studies, and these results can help explain similar oscillations observed in modeling and behavioural studies as a consequence of using a proportional controller with high controller gain.

The mean error of the step response (Fig. 3.7c) also highlights the effect that asymmetric sensitivity of a single sensor (H1) has on the performance of compensating for a constant perturbation. Man-made sensors such as accelerometers and gyroscopes typically have symmetric sensitivities around a zero set point. As proposed
earlier, the asymmetry in the H1 cell might serve a functional role in the context of optomotor control as the asymmetry is suggested to help the fly during tasks involving visual fixation \cite{Wolf and Heisenberg, 1979}. On the other hand, spontaneous spike rates $F_s$ were shown to increase in the blowfly visual interneurons depending on the locomotor state with higher activity observed during motion versus rest \cite{Longden and Krapp, 2010, 2009}. This increased activity $F_s$ reduces the asymmetry with which the H1 cell encodes PD and ND motion, respectively. This predicts that the asymmetry in mean error around any constant perturbation would be lower for flies when they are either walking/flying as compared to when they are stationary. Furthermore, recent studies have shown that the temporal frequency tuning of visual interneurons (HSN,H1) are increased towards higher values when the animal is walking/flying versus at rest \cite{Chiappe et al., 2010, Jung et al., 2011}. Since the FRI uses signals from the H1-cell in an immobilized fly to correct for the visual slip-speeds under closed-loop conditions, its performance is better suited for lower versus higher temporal frequencies (c.f. Fig 3.9). The results from the work by Chiappe et al. \cite{2010} and Jung et al. \cite{2011}, however, predicts that the closed-loop correction of slip-speeds using neural signals from flies that are induced into locomotor states such as walking or flying, would result in a peak performance of the FRI at higher temporal frequencies than the ones observed when the animal is at rest. Ultimately, since the FRI uses neural signals recorded from an immobilized fly, the effect of locomotor state on the performance of the FRI under closed-loop conditions cannot be directly estimated and can only be predicted at this point (c.f. section 6.3).

The bode plot (Fig. 3.9) of the FRI frequency response exhibits low-pass filter characteristics which probably reflects the transfer function of the actuator (in this case the robot and the turn-table). Low-pass filters are often used to model actuator properties in studies on insect sensori-motor control \cite{Warzecha and Egelhaaf, 1996, Lindemann et al., 2008}. For the FRI, the robot has the additional advantage of having real-world dynamics which are not captured by previous optomotor studies in blowflies which simply use a static low-pass filter as a model for the actuator compensating for closed-loop visual perturbations.

From the performance index $J_i$ calculated for different $K_p$ values (Fig. 3.10), it
can be concluded that no specific value of $K_p$ provides optimal performance over the entire frequency range $f_i$. Instead, optimal performance is achieved by specifically tuning the controller gain $K_p$ for different frequencies $f_i$. During free flight, a fly encounters a highly dynamic visual stimulus range, in terms of angular velocity and accelerations. To achieve optimal performance over an extended dynamic range, the results predict that the best strategy for the fly would be to continuously adapt the controller gain depending on the angular velocities and accelerations it encounters. For a visual input with a constant angular velocity or low angular accelerations, the rise time is not a critical parameter for minimizing the slip-speed which means a comparatively low controller gain can be used. A high controller gain is necessary for the stabilization of visual inputs with high angular acceleration components. Increasing the controller gain however has to be carefully balanced as the benefits of fast rise times are at the expense of energy lost due to oscillations about the desired set point.
4. Adaptive gain control strategy for visuo-motor stabilization

In Chapter 3, the closed-loop dynamics of the fly-robot interface were characterized for the case where a proportional feedback controller was implemented. Because no single value of the controller gain was able to perform visual stabilization optimally over the frequency range tested, an implementation of a continuously adapting feedback controller may be a strategy to improve the performance of the system. In this chapter, an adaptive controller is presented that alters its closed-loop gain based on the response dynamics of the H1 cell. The resulting dynamics of the fly-robot interface are characterized and the performances of the adaptive and proportional controllers in stabilizing the visual input to the fly are compared.

4.1. Adaptive gain control

Closed-loop results obtained with the fly-robot interface using a proportional controller showed that no single value for the controller gain was able to provide optimal performance within the frequency range tested (cf. Chapter 3). Depending on the input frequency, different values of controller gain were found to minimize the relative motion between the robot and the visual surroundings.

Proportional controllers belong to a generic family of feedback systems called Proportional-Integral-Derivative or PID controllers that are most commonly used in many technical applications. Traditionally, the parameters of a PID controller, the
proportional ($K_p$), integral ($K_i$) and derivative ($K_d$) gains are estimated over the desired operating range, either manually or using automated methods e.g. [O’Dwyer, 2006]. These parameters, however, remain constant throughout the control task. Furthermore, while using PID controllers for linear systems might provide a good performance over the desired operating range, it does not guarantee optimal control for nonlinear systems. For flies, although the behavioural output measured for optomotor tasks has been shown to be approximately linear [Graetzel et al., 2010; Taylor and Krapp, 2007], at several stages, along the sensorimotor pathway nonlinear neuronal processing takes place [Borst et al., 2003; Reisenman et al., 2003]. The use of a proportional controller to stabilize the visual input to a highly nonlinear system therefore may not guarantee optimal control.

In the case of the optomotor response in flies, proportional controllers have been used in flight simulators to close the loop between the visual input and an output parameter produced by the animal. In these studies, either the fly’s behavioural output (yaw torque, thrust or differential leg activity [Mayer, 1989; Wolf et al., 1992; Wolf and Heisenberg, 1990]) or their neural activity (differential H1 signal [Warzecha and Egelhaaf, 1996]) have been used to obtain a proportional feedback signal that was used to stabilize the pattern motion.

In contrast to proportional controllers, adaptive controllers are not restricted to static controller parameters. Instead, adaptive controllers adjust the parameters of control, in this case the feedback gain, based on the input to the controller. Adaptive controllers can operate in feedback or feed-forward mode and may be used to control both linear and nonlinear systems. In the next section, an adaptive controller to close the loop for the FRI is described that is inspired by the input-output re-scaling properties of Large Monopolar Cells (LMCs) in the fly.

### 4.1.1. Description of the adaptive controller

A limited dynamic output range and the inherent background noise limits a neuron’s ability to effectively encode a sensory stimulus. In order to prevent loss of information, a neuron has to apply the appropriate weights to the input stimulus in order to efficiently represent the input. Laughlin [1981] showed that in large
monocular cells (LMCs) in the peripheral visual pathway of the fly the input signals are weighted according to a cumulative probability function of the stimulus intensities. The cumulative probability function maximizes the information capacity of the neuron, which enables an optimal representation of the sensory stimulus (Fig 4.1). While this function is optimal for a given stimulus distribution, visual interneurons such as the LMC experience a very wide distribution of stimuli over the course of a day. The response range of the neuron is not sufficient to encode the entire range of stimuli, which requires an adaptive coding strategy.

Laughlin [1994] presents two conditions necessary for an adaptive coding strategy to maximize information transmission (i) the stimulus-response function should have a sigmoid shape and (ii) the slope at the midpoint of the curve can be altered dynamically to scale the input-output relationship. This neural coding strategy for maximizing the representation and transmission of information in LMC neurons was used as an inspiration for the design of an adaptive closed-loop controller for the fly-robot interface.

The modified block diagram for the fly-robot interface with the adaptive controller is shown in Fig 4.2. Apart from the implementation of an adaptive controller, the structure of the closed-loop system remains the same i.e. the sensor (fly H1 LPTC) and actuator (robot) control blocks are the same as in Figure 4.2b (cf Chapter 3). As described in the previous chapter for the proportional controller, relative motion between the turntable and the robot induce retinal image shifts over the fly’s eyes (slip-speed) which modulates the spiking activity of the H1 cell. The instantaneous spiking rate, \( F \), is determined and mapped onto a compensation error, \( E \), by the adaptive controller to be sent to the robot. The compensation error, \( E \), is then used to update the robot speed \( V_r \) using a proportional controller with \( K_p = 1 \).

For the proportional controller, the function used to map the instantaneous spiking rate, \( F \), onto the compensation error, \( E \), did not change over time. The initial scaling of the curve was determined by the maximum spiking rate, \( F_{\text{max}} \), calculated under open-loop conditions. With the proportional controller, the function transforming the spiking rate into a compensation error only partly fulfilled the second condition set out by Laughlin [1994], i.e. while the mapping function had a sigmoid shape, the gradients at the curve’s midpoint in both the preferred (PD) and
null direction (ND) were static.

The adaptive controller implements variable slope at the mid-point of the sigmoid mapping function proposed by Laughlin by continually estimating the maximum spiking rate, $F_{\text{max}}$, and re-scaling the sigmoid curve to alter the input-output relationship between the spiking rate, $F$, and the compensation error, $E$. Fig 4.3a illustrates how the adaptive controller estimates $F_{\text{max}}$, from the H1 spiking rate ($F(\tau)$) over the time window $t - \Delta T_{ws} \leq \tau \leq t$. $F_{\text{max}}$ is estimated as:

$$F_{\text{max}} = \max \{F_s, F(\tau)\}$$  \hspace{1cm} (4.1)

where $F$ and $F_s$ are the estimated and spontaneous spiking rates respectively and $t - \Delta T_{ws} \leq \tau \leq t$ is the causal time interval over which $F_{\text{max}}$ is estimated.

The time interval used to dynamically estimate $F_{\text{max}}$ is determined by the window size $\Delta T_{ws}$ which is the only parameter used by the adaptive controller. During
Figure 4.2.: Block diagram of closed-loop fly-robot interface using the (a) adaptive and (b) proportional controller. (a) Apart from a change in the feedback controller, all other components of the closed-loop system are the same as in (b). As described previously with the proportional controller, the relative motion (slip speed) between the turntable and the robot $\omega_p - \omega_r$ causes spiking in the H1 cell at an instantaneous rate $F$. The conversion from the spiking rate $F$ to the compensation error $E$ for the adaptive controller can be dynamically scaled based on the instantaneous measurements of the maximum spiking rate $F_{\text{max}}$ over a window with window size $\Delta T_{ws}$ (for a detailed description see Fig 4.3a).

Closed-loop operation, $F_{\text{max}}$ is estimated over the time interval $\Delta T_{ws}$ every 50 ms (discrete control loop delay). The estimated value of $F_{\text{max}}$ over the time interval is then used to dynamically re-scale the sigmoid mapping of the spiking rate, $F$, on to the compensation error, $E$ (see Fig 4.3b). The sigmoid curve can be divided into two mapping regions, the PD $(F_s, F_{\text{max}})$ and the ND $(0, F_s)$. Since the spontaneous spiking rate $F_s$ for the H1 cell is assumed to be unaffected by visual motion, the sigmoid curve for the ND mapping region $(0, F_s)$ was not re-scaled. However, for motion in the PD, when the estimate for $F_{\text{max}}$ is large (time window 3 in Fig 4.3a), the sigmoid for mapping function for the PD region $(F_s, F_{\text{max}})$ is stretched along the horizontal axis which reduces the slope at the midpoint of the curve.
Figure 4.3.: Re-scaling of the spiking rate, $F$, mapped onto the compensation error, $E$, for the adaptive controller. (a) Every 50 ms, $F_{\text{max}}$ is estimated over the time interval $t - \Delta T_{ws} \leq \tau \leq t$, where the window size $\Delta T_{ws}$ is a control parameter for the adaptive controller (b) The estimated value of $F_{\text{max}}$ is used to dynamically re-scale the sigmoid function mapping the spiking rate, $F$, on to the compensation error, $E$ (only in the PD).

When the estimate for $F_{\text{max}}$ is small (time window 2 in Fig 4.3a), the sigmoid for the mapping region PD ($F_s, F_{\text{max}}$) is compressed along the horizontal axis which increases the slope at the midpoint of the curve. This dynamic re-scaling applies a coding strategy similar to that proposed by Laughlin [1994], in that it increases and/or decreases the slope of the midpoint of the sigmoid mapping function and thus adjusts the sensitivity to changes in the spiking rate.
Once the value for $F_{\text{max}}$ has been estimated over the time interval $t - \Delta T_{ws} \leq \tau \leq t$, the spiking rate of the H1 cell, $F$, is converted into the compensation error, $E$, using the same equations for the mapping function $F \rightarrow E$ as defined in Chapter 3:

$$E = \begin{cases} 
-\frac{F_{\text{max}}}{2} \{ \cos(2\pi\phi) + 1 \} \left\{ \frac{1}{4} \left(V_r(t) - \hat{V}_r \right) \right\} & \text{for } F < F_s, \\
0 & \text{for } F = F_s, \\
\frac{F_{\text{max}}}{2} \{ \cos(2\pi\phi) + 1 \} & \text{for } F > F_s,
\end{cases}$$

where, $\phi = -\frac{1}{2} \left( \frac{F}{F_{\text{max}}} \right)$

Here $\hat{V}_r$ is a speed signal offset that is required to initiate robot rotation i.e. the minimum speed signal to overcome the robot’s inertia.

The estimated compensation error, $E$, is then used to update the robot speed:

$$V_r(t+1) = E + V_r(t),$$

with the angular velocity of the robot given by:

$$\omega_r = G(s) \cdot V_r,$$

and where $G(s)$ is the transfer function of the robot which is:

$$G(s) = \frac{1.73}{s^2 + 1.87s + 0.86}$$

### 4.1.2. Closed-loop experiments

As for the proportional controller described in Chapter 3, the step and frequency responses of the fly-robot interface with the adaptive controller under closed-loop conditions were obtained using an adaptive controller. The responses for the adap-
tive controller were obtained with \( N = 5 \) flies for \( \Delta T_{ws} = [0.05, 0.10, 0.15] \) s and with \( N = 6 \) flies for \( \Delta T_{ws} = 0.50 \) s. The same step and sinusoidal input stimuli were applied for both the proportional and the adaptive controller in order to compare the closed-loop performance of the two types of control laws. The step response stimulus was delivered by the turntable as:

\[
\omega_p = \begin{cases} 
0 & \text{for } t < 2.5 \text{ s}, \\
144 \text{ deg/s} & \text{for } t \geq 2.5 \text{ s},
\end{cases}
\]

A sine-wave with a DC-offset was used to characterize the closed-loop frequency response:

\[
\omega_p = 72 [\sin(2\pi f_i t) + 1]
\]

where the input frequency range \( f_i \) was defined as \( 0.03 \leq f_i \leq 3.0 \) Hz.

### 4.2. Frequency response characterization

#### 4.2.1. Sample responses

Sinusoidal inputs at frequencies \( f_i \) over the range \( 0.03 \leq f_i \leq 3.0 \) Hz were used to characterize the performance of the fly-robot interface with the adaptive controller and the results were compared with those obtained with the proportional controller in Chapter 3.

Fig 4.4 (upper left and right panel) shows two sample traces of the turntable movement (blue traces) and the compensatory movements of the robot (green traces) plotted over time for the adaptive controller. For \( \Delta T_{ws} = 0.10 \) s, the robot compensated better for the imposed turntable motion compared to the condition where \( \Delta T_{ws} = 0.50 \) s. Rather than generating smooth movements, the compensatory rotations of the robot were superimposed by 1 Hz oscillations. 1 Hz was previously identified (see Chapter 3) as the natural frequency of the fly-robot interface under proportional control. Similar oscillations at this frequency were observed in the robot responses for both \( \Delta T_{ws} = 0.10 \) s & 0.50 s (see Fig 4.4c). Increasing \( \Delta T_{ws} \) from 0.10 s to 0.50 s decreases the power at the input frequency \( (f_i = 0.1 \text{ Hz}) \) while
Figure 4.4.: Examples of turntable versus robot responses upon sinusoidal inputs for the adaptive controller (a-b) Sample turntable and robot responses angular velocities for a sinusoidal input ($f_i = 0.1$ Hz) and time window $\Delta T_{ws} = 0.10$ s & 0.50 s. For $\Delta T_{ws} = 0.10$ s, the robot compensates for the turntable response well and minimizes the visual slip-speed observed by the fly. Increasing $\Delta T_{ws} = 0.5$ s decreases the performance of the robot in compensating for the imposed rotation of the turntable. (c) The power spectrum of the robot responses in (a) & (b). Increasing $\Delta T_{ws}$ from 0.10 s to 0.50 s decreases the power at the stimulation frequency ($f_i = 0.1$ Hz) while slightly increasing the power at the natural frequency (1 Hz).

The responses of the robot for the adaptive and the proportional controller are compared in Fig 4.5. Panels (a-c) in Fig 4.5 show the robot responses to sinusoidal in-
Figure 4.5.: Comparison of turntable versus robot responses upon sinusoidal inputs ($f_i = 0.3$ Hz) for the (a) adaptive and the (b,c) proportional controllers. (a-b) The robot is able to compensate well for the imposed turntable rotation for the adaptive controller ($\Delta T_{ws} = 0.10$) and the proportional controller ($K_p = 0.5$). (c) For the proportional controller with low gain ($K_p = 0.1$), the robot response has a phase delay with respect to the turntable rotation. (d) The power spectrum for the adaptive and the proportional controller for $\Delta T_{ws} = 0.10$ s and $K_p = 0.5$ are similar with high power at the stimulation frequency $f_i = 0.3$ Hz and the natural frequency $f = 1$ Hz. The power at the stimulation frequency for the proportional controller with $K_p = 0.1$ Hz is also high, but with lower power at the natural frequency, possibly because of the phase lag between the robot the turntable response for this value of the controller gain.
puts at a frequency $f_i = 0.3$ Hz. The robot compensates for the imposed turntable motion with minimal phase lag for the adaptive controller with $\Delta T_{ws} = 0.10$ s and the proportional controller with $K_p = 0.5$. When the controller gain for the proportional controller is reduced to $K_p = 0.1$, the robot response amplitude also decreases and a phase difference between the turntable motion and robot response can be observed (Fig 4.5c). The power spectra for the adaptive and the proportional controllers (Fig 4.5d) show the power of the robot responses at the input frequency (0.3 Hz) and the natural frequency (1.0 Hz) for the two controllers. The power distributions at the input (0.3 Hz) and the natural frequency (1.0 Hz) for the adaptive controller with $\Delta T_{ws} = 0.10$ s and the proportional controller with $K_p = 0.5$ are similar. Decreasing the controller gain for the proportional controller slightly decreases the power at the input frequency while significantly decreasing the power at the oscillation or natural frequency. For the proportional controller, it was shown in Chapter 3, that increasing the controller gain $K_p$ increased the oscillations observed at the natural frequency causing reduced power at the stimulation frequency. For the adaptive controller significant power at the natural frequency therefore indicates that it is operating as a proportional controller with high controller gain $K_p$. However, this increased power at the natural frequency for the adaptive controller is not at the expense of power at the input frequency and a reduction in the ability of the robot to compensate for the turntable movements.

### 4.2.2. Bode magnitude and phase plots

To characterize the frequency response of the fly-robot interface with the adaptive controller, sinusoidal inputs at frequencies in the range $0.03 \leq f_i \leq 3.0$ Hz were used. The results were compared to those obtained with the proportional controller. Fig 4.6 shows the bode magnitude and phase plots for both the adaptive and the proportional controllers. The gain plot (Fig 4.6a) for the adaptive controller shows a low-pass filter behaviour for all values of $\Delta T_{ws}$, with a smoother roll-off for $\Delta T_{ws} = [0.05, 0.10, 0.15]$ s compared to $\Delta T_{ws} = 0.50$. The system gains for the adaptive controller with $\Delta T_{ws} = [0.05, 0.10, 0.15]$ s are higher than those for $\Delta T_{ws} = 0.50$ s across the entire frequency range except for 1 Hz. The system gain for the adap-
tive controller with $\Delta T_{ws} = [0.05, 0.10, 0.15]$ s is higher than that observed for the proportional controller with high feedback or controller gain ($K_p = 1.0$) but lower than that observed with the controller gain $K_p = 0.5$. However, over the tested frequency range, the adaptive controller is less affected by the resonator (1 Hz)/anti-resonator (0.6 Hz) phenomenon observed with the proportional controller. The impact of the natural frequency (1 Hz) on the system gain for the adaptive controller is considerably smaller than it is on the gain of the proportional controller over the range $0.6 \leq f_i \leq 1.0$.

Similarly for the phase, a low controller gain $K_p$ for the proportional controller leads to an increased phase shift between turntable motion and the compensatory response of the robot. In comparison, the adaptive controller for all values of $\Delta T_{ws}$ has a phase profile similar to that of the proportional controller with high controller gain ($K_p = 1.0$). This results in the adaptive controller responding faster to any changes of the visual input which modulates the spiking rate of the H1 cell, while maintaining a high system gain over the entire frequency range $f_i$.

Adaptive control maximizes motor output bandwidth at the cost of optimal visual compensation

The system gains of both the adaptive and the proportional controller had low-pass filter characteristics. Low-pass filters can be characterised by a combination of the pass-band gain, $G_{dc}$, and the cut-off frequency, $f_c$ (Fig 4.7) [Ogata 1997]. $G_{dc}$ is the system gain in the flat pass-band region of the filter, while $f_c$ is the frequency at which the system gain first drops below $-3$ dB relative to $G_{dc}$, or half the maximum power in the filter pass-band. In the case of the frequency response curves obtained for the adaptive and proportional controllers (Fig 4.6), the bandwidth of the system is equivalent to $f_c$.

Fig 4.8 shows $f_c$ and $G_{dc}$ for both the adaptive and proportional controllers. For all controller parameters, the adaptive gain controller had larger bandwidth than the proportional controller (Fig 4.8a & 4.8b). For the adaptive gain controller with $\Delta T_{ws} = [0.05, 0.10, 0.15]$ s, the bandwidth (0.5 Hz) was the maximum achievable given the limitations imposed by the robot dynamics (cf. Chapter 2) while the pass-
Figure 4.6.: Bode magnitude and phase plots for the adaptive (a,c) and proportional (b,d) controller. The responses for both controllers were probed over the frequency range $0.03 \leq f_i \leq 3 \text{ Hz}$. The magnitude plot of the adaptive controller (a) shows low-pass filter characteristics for all $\Delta T_{ws}$ with similar properties for $\Delta T_{ws} = 0.05, 0.10 \& 0.15 \text{ s}$. The magnitude plots for the adaptive controller do not exhibit sharp peaks at the natural frequency (1 Hz) of the fly-robot interface which are clearly visible for the proportional controller (b) for $K_p = 0.1, 0.5 \& 1.0$. (c) The phase profiles of the adaptive controller for all $\Delta T_{ws}$ are nearly identical with the phase profiles of the proportional controller for a higher gain $K_p = 1.0$ (d).

band gain was above the $-3 \text{ dB}$ absolute cut-off value (Fig 4.8c). For $\Delta T_{ws} = 0.50 \text{ s}$, the bandwidth ($\approx 1\text{ Hz}$) was artificially large due to the very low corresponding pass-band gain ($< \frac{1}{4}$ the peak power measured for any controller configuration tested). The bandwidth for the proportional controller for all $K_p$ was less than
Figure 4.7.: DC system gain and bandwidth for an ideal low-pass filter. The DC system gain for the ideal filter is the steady-state gain for the pass band ($G_{dc} = 0$ dB) while the cut-off frequency and the bandwidth of the system are both 1 Hz.

0.5 Hz (Fig 4.8b). However, for $K_p = [0.1, 0.5]$, the proportional controller had a higher pass-band gain than the adaptive gain controller for all $\Delta T_{ws}$ (Fig 4.8d). On the other hand, distortions in the frequency response due to the system’s natural frequency were more pronounced for the proportional controller with $K_p = [0.1, 0.5]$. To summarize, characterization of the pass-band gain and bandwidth based on the frequency response shows that the adaptive gain controller maximized the output bandwidth at the cost of system gain.

**Performance Index**

The performance index introduced in Chapter 3, is a convenient measure to compare the performance of the proportional and adaptive controllers over the range of frequencies $f_i = [0.03, 0.1, 0.3, 0.6, 1.0]$. For $f_i = 3$ Hz, the performance index is disregarded since the system gain at this frequency is very low (see Fig 4.6). As
Figure 4.8.: Bandwidth and DC-gain of the adaptive (a,c) and the proportional controllers (b,d) respectively. The bandwidth for both controllers are calculated for the $-3$ dB cut-off frequency level. The adaptive controller has a higher bandwidth for all $\Delta T_{ws}$ as compared to the proportional controller, with the highest bandwidth for $\Delta T_{ws} = 0.50$ s. The DC system gains $G_{dc}$ (calculated as the system gain at $f_i = 0.03$ Hz) are shown for the adaptive (c) and the proportional (d) controllers. The system gains for the adaptive controller for all $\Delta T_{ws} = [0.05, 0.10, 0.15]$ s are above the absolute $-3$ dB cut-off but lower than the optimal observed with the proportional controller for $K_p = [0.1, 0.5]$.

with the proportional controller, the performance index, $J_i$, is defined as:

$$J_i = \frac{1}{T_i} \left( \alpha_F \cdot J_{in}^i + \alpha_{slip} \cdot J_{out}^i \right)$$  \hspace{1cm} (4.2)
where $T_i$ is the total time of the closed-loop measurements, $\alpha_F$ and $\alpha_{slip}$ are the associated input and output weights and $J_{in}^i$ and $J_{out}^i$ are the energy of the spike rate (input) and the slip-speed (output) signals, respectively, measured at the input frequency $f_i$.

\[ J_{in}^i = \int_0^\infty F_i^2 \, dt \quad (4.3) \]

\[ J_{out}^i = \int_0^\infty \left( \omega_p^i - \omega_r^i \right)^2 \, dt \quad (4.4) \]

Thus, $J_i$ provides a cost function which is an estimate for the total energy spent by the sensor (H1 cell) to reduce the retinal slip-speed. An optimal controller would minimize $J_i$ over the desired operating range. The performance index, $J_i$, for both the adaptive and the proportional controller are shown in Fig. 4.9 for the case where the cost for the sensor signals and cost for the compensation signals are balanced ($\alpha_F = \alpha_{slip} = 0.5$).

For the adaptive controller, increasing the input frequency, $f_i$, increases $J_i$ for all
The optimal performance of the adaptive controller is achieved with $\Delta T_{ws} = 0.10\ s$ for $0.03 \leq f_i \leq 0.3$ and $\Delta T_{ws} = 0.05$ for $0.6 \leq f_i \leq 1.0$. The difference in performance of the adaptive controller for different values of $\Delta T_{ws} = [0.05, 0.10, 0.15]$ s is negligible compared to the changes in performance observed for the proportional controller with different $K_p$. Furthermore, the peak performance (minimization of $J_t$) of the adaptive controller compares favourably to that of the proportional controller over all input frequencies $f_i$ and all combinations of the controller parameters $\Delta T_{ws}$ and $K_p$.

### 4.3. Step Response Characterization

The step responses of the closed-loop adaptive controller were characterized in a similar way to those of the proportional controller. Fig 4.10 shows the step input functions of the turntable and the mean compensatory robot responses for an adaptive controller with $\Delta T_{ws} = 0.05, 0.10, 0.15, 0.50\ s$. The mean responses of the adaptive controller show increased activity prior to the step input ($t = 2.5\ s$) compared to the proportional controller. Prior to the step input being presented there is no visual motion observed by the fly. This results in a low estimate for $F_{max}$ within the time interval $t - \Delta T_{ws} \leq \tau \leq t$ which leads to an increased sensitivity to changes in spiking rate, $F$. This increased sensitivity in combination with inherent variations of the spontaneous spiking rate of the H1 cell results in small jerk-like motions of the robot prior to the step input. This is in contrast to the proportional controller which uses a static gain $K_p$ and an estimate of $F_{max}$ in open-loop, which results in little or no observed motion in the robot response prior to the step input ($t = 2.5\ s$).

A comparison of the performance parameters during with the step responses of the adaptive and proportional controllers is shown in Fig 4.11. As for the proportional controller in Chapter 3, the rise time, percentage overshoot and mean error in both the null and preferred direction were calculated for the adaptive controller.

For the adaptive controller, increasing $\Delta T_{ws}$ from 0.05 s to 0.10 s slightly decreases the rise time of the robot response (see Fig 4.11a) with the rise times obtained.
for $\Delta T_{ws} = [0.10, 0.15]$ s being comparable to the minimum achievable ones for the proportional controller $K_p = [0.5, 1.0]$. Increasing $\Delta T_{ws}$ beyond 0.10 s increases the rise times again. On the other hand, increasing $\Delta T_{ws}$ decreases the percentage overshoot of the adaptive controller (see Fig 4.11c). In the range $0.05 \leq \Delta T_{ws} \leq 0.15$ s, increasing $\Delta T_{ws}$ generally decreases both the rise time and the percentage overshoot of the adaptive controller. However, a trade-off between rise times and percentage overshoot exists when increasing $K_p$ in the proportional controller. While increasing $K_p$ decreases the rise times (see Fig 4.11b), it also increases the percentage overshoot (see Fig 4.11d). Obviously, a decrease in both rise time and percentage overshoot would be advantageous from a control perspective for the fly when performing visuo-motor tasks. While changing control parameters of the proportional controller results in competing benefits related to rise times and percentage overshoot, the adaptive controller does not suffer from such limitations.

The mean error observed with the adaptive controller shows a stronger asymmetry (see Fig 4.11c) than that obtained with the proportional controller (see Fig 4.11f). The combined mean errors with the adaptive controller for all $\Delta T_{ws}$ are larger than those of the proportional controller with $K_p \geq 0.1$. However, the adaptive controller decreases the mean error for motion in the preferred direction where as the proportional controller does not.

To summarize the effects that the controller parameters have on the two controllers: compared to the proportional controller, within a certain range of $0.05 \leq \Delta T_{ws} \leq 0.15$, the adaptive controller does not suffer from performance trade-offs as a result of changing the control parameter.
Figure 4.10.: Mean step response of the fly-robot interface for the adaptive controller. The turntable was given a step input angular velocity with a DC value of $\omega_p = 144 \text{ deg/s}$. Mean and standard deviation of the robot responses with the adaptive controller are shown for $\Delta T_{ws} = [0.05, 0.10, 0.15, 0.50] \text{ s}$. 
Figure 4.11.: Comparison of step response performance of adaptive and proportional controllers. (a) Rise time for the adaptive controller decreases with increasing $\Delta T_{ws}$ within the range $0.05 \leq \Delta T_{ws} \leq 0.15$ s (b) Rise time for the proportional controller decreases with increasing $K_p$ (c) Percentage overshoot for the adaptive controller decreases with increasing $\Delta T_{ws}$ while for the proportional controller (d) it increases with increasing $K_p$ (percentage overshoot is calculated as $\hat{\omega}_r - \omega_p$ where $\hat{\omega}_r$ is the peak of the robot response as it initially exceeds the step input) (e) Combined mean error for the adaptive controller for $0.05 \leq \Delta T_{ws} \leq 0.15$ s is greater than with the proportional controller with $K_p \geq 0.1$. However, the mean error in the preferred direction for the adaptive controller is less than that of the proportional controller for all values of $\Delta T_{ws}$ and $K_p$. (Mean error is measured as $\frac{1}{T S} \sum |\omega_p - \omega_r|$, where $T$ is the time window over which the error is calculated and $S$ is the sampling rate of turntable and robot signals.)
4.4. Discussion

In this Chapter, the FRI was used to characterize the optomotor yaw response in the blowfly with an adaptive controller. While there have been many studies on neural coding of motion information in the blowfly (for review see Borst and Haag [2002], Krapp and Wicklein [2008]), the mechanisms that convert sensory signals into motor commands under closed-loop conditions, are still poorly understood (see Theobald et al. [2009]). As mentioned earlier, this is primarily due to methodological limitations with obtaining neural recordings in freely behaving animals. Here, the frequency response dynamics of a visuo-motor control task in a FRI were characterized using two different feedback controllers, which transform neural signals into motor commands. The two closed-loop controllers characterized were a static gain (proportional) and an adaptive gain controller.

The FRI used spiking activity of the H1 cell to control the compensatory rotation of a robot emulating an optomotor response. The H1 cell belongs to a specific class of hetero-lateral neurons that connect the two hemispheres of the fly brain with each other [Hausen, 1976, Krapp, 2007]. This connection enables the integration of binocular motion information which increased the detection of specific self-motion components. The H1 cell provides excitatory input to the contra-lateral horizontal equatorial cell (HSE), a directionally selective output neuron that has been suggested to encode yaw rotations around the fly’s vertical axis [van Hateren et al., 2005, Kern et al., 2005]. While optomotor control mechanisms were observed to be linear at the behavioural level [Theobald et al., 2009, Graetzel et al., 2010], the responses of the H1 cell are highly non-linear [Borst et al., 2003]. The mechanisms by which nonlinear neuronal signals are combined to result in an overall linear performance of the system at the behavioural level are still not fully understood.

A possible control strategy for the yaw optomotor response of the fly would be to employ a proportional controller with a static feedback gain $K_p$ that is based on the activity of neurons sensitive to horizontal motion, including those of the H1 cell. However, optimal $K_p$ differs depending on the input frequency and no single value of $K_p$ was able to minimize the retinal slip speed under closed-loop conditions (Fig 4.6b). This is likely to be due to the relationship between $K_p$ and the
overall systems behaviour (cf. Chapter 3). A lower $K_p$ leads to longer rise time but a smaller steady state error and overshoot. This makes it ideal to compensate for externally forced perturbations which result in slow accelerations of the visual input. However, to compensate for high accelerations a higher $K_p$ is required to achieve fast rise times of the controller. Fast response times are particularly important for reflexes such as the optomotor response so that the fly is able to compensate for slip-speeds with high acceleration while maintaining stable feedback control. However, although higher $K_p$ decrease the response times for the system, they may cause control oscillations, leading to a resonator/anti-resonator phenomenon in the frequency response (Fig 4.6b).

An alternative visuo-motor control strategy might be to dynamically scale the feedback gain at which H1 cell activity is converted into optomotor yaw torque. The adaptive gain controller presented in this chapter is such an example. While there are many ways to implement an adaptive gain controller, the choice of controller in this chapter was inspired by the matched coding strategy proposed by Laughlin (1994) to maximize information transmission from fly photoreceptors to large monopolar cells. Laughlin identified two conditions necessary for an adaptive coding strategy: (i) the stimulus-response function should have a sigmoid shape and (ii) the slope at the midpoint of the curve can be altered dynamically to scale the input-output relationship. For the proportional controller, the function used to map the instantaneous spiking rate, $F$, onto the control input, $E$, was static. The initial scaling of the curve was determined by the maximum spiking rate, $F_{\text{max}}$, calculated under open-loop conditions. With the proportional controller, the function transforming $F$ onto $E$ only partly fulfilled the second condition above. While the mapping function had a sigmoid shape, the slope at the curve’s midpoint in both the preferred and null directions were static. The adaptive gain controller complies with the second condition proposed by Laughlin in that it continuously re-scales the sigmoid relationship between $F$ and $E$ by continually estimating and updating $F_{\text{max}}$.

In behavioural studies, Egelhaaf (1987) visually stimulated *Musca domestica* with oscillating patterns and observed that the yaw torque had low-pass filter characteristic. For low input frequencies, $f_i \leq 0.0625$ Hz, the measured yaw torque was
approximately constant. However, increasing the input frequency beyond 0.0625 Hz resulted in the yaw torque declining approximately linearly. Beyond $f_i = 4$ Hz, the measured yaw torque response was nearly zero. In the closely related species *Calliphora* Borst (2003) observed similar low-pass filter characteristics in the response of the H1 cell to white-noise stimuli but at a significantly higher cut-off frequency ($f_c = 20$ Hz). From the two studies, it can be concluded that the bandwidth of the visual sensor, the H1 cell, is considerably higher than that of the motor system. Ultimately, in a freely moving fly, the frequency response of visuo-motor behaviours is limited by the dynamics of the motor systems [Graetzel et al. 2010].

For the optomotor response the limits would depend on the flight motor system in combination with the animal’s aerodynamic properties, both of which contribute to the animal’s yaw response. Consequently, the higher priority for the fly would possibly be to maximize the bandwidth of the motor system as compared to that of the sensory systems, in this case the visual system. This would lead one to opinion that any control strategy that does not maximize the motor system bandwidth would be operating sub-optimally.

Maximizing the pass-band gain and bandwidth offer functional advantages for the fly in an attempt to stabilize its body attitude based on visual motion information under closed-loop conditions. A higher pass-band gain would more efficiently reduce any retinal slip speed over the fly’s eyes and would therefore increase the stabilization performance. Similarly, a higher cut-off frequency or bandwidth means that the fly would be able to stabilize visual motion over a larger dynamic input range. In the case of the FRI, the frequency response properties are limited by the dynamics of the robot. For the robot, the maximum achievable frequency response bandwidth is 0.5 Hz. While the proportional controller is able to achieve near perfect compensation in the pass-band region for $K_p = 0.1$ & 0.5 (Fig 4.8d), the corresponding bandwidth of the motor actuator i.e. the robot is sub-optimal (Fig 4.8b). In contrast, the bandwidth of the motor actuator for the adaptive gain controller is approximately equal to the maximum possible with the robot dynamics. However, while the adaptive gain controller is able to maximize the bandwidth of the motor actuator, it does so at the slight expense of the pass-band gain. This is consistent with the proposition that sensory systems of the fly encode differences rather than absolute values [Taylor and Krapp 2007] and that perfect compensation
might not be required as long as the visual slip-speed remains within the sensory bandwidth limits. The adaptive gain controller also manages to keep the phase differences lower than the proportional controller does (Fig 4.6c). This is extremely important for stable control as an increased phase difference can lead to unwanted oscillations that increase the visual slip-speed observed by the fly. Additionally, the overall performance of the adaptive gain controller in minimizing the visual slip-speed compares favourably to that of the proportional controller as measured in the time domain by the performance index (Fig 4.9).

Two conclusions can be drawn from the work presented with the FRI in this paper. Firstly, no single control strategy works equally well for all input frequencies; i.e. both static and adaptive gain feedback controllers have benefits and drawbacks. The best proposed strategy for the flies would be to adjust the control laws and/or parameters depending on the stimulus dynamics. Secondly, to fully understand the closed-loop sensorimotor performance in the fly, all component systems must be fully characterized; i.e. sensory and motor systems as well as the feedback control laws and delays. Under closed-loop conditions, the bandwidth of sensory and motor systems will have a bearing on one another and must therefore be considered as a cohesive system and not looked at in isolation.
5. Neural responses under closed-loop conditions

In Chapters 3 and 4, the fly-robot interface (FRI) was used in closed-loop to investigate its performance in a visual stabilization task. A turn-table was used to introduce external visual perturbations into the closed-loop system and the corresponding robot responses were measured. The turn-table and robot angular velocities were used to quantify the performance of the fly-robot interface with a closed-loop proportional (static gain) and adaptive gain controller. In this chapter, the dynamics of the spiking activity of the H1-cell, with both the proportional and the adaptive gain controllers, were studied under closed-loop conditions.

5.1. Adaptive re-scaling properties of the H1-cell

Neurons are required to process and encode sensory stimuli while operating under strict energy constraints [Laughlin, 2001; Laughlin et al., 1998]. The neuronal responses i.e. the neural codes, have been proposed to efficiently represent stimulus qualities such as local image contrast of image velocity [Barlow, 1993; Attneave, 1954]. In the context of optic flow processing, image contrast- and size dependent responses are un-desirable [Straw et al., 2008; Barnett et al., 2010]. In order to counter this, there are contrast gain control and dendritic gain control mechanisms in place to reduce the contrast dependent component of neural responses which could otherwise drive the output of the cell into saturation [Harrison et al., 2000; Borst et al., 1995].
In the case of large monocular cells (LMCs) in the early visual pathway of the fly, matching the neuronal coding strategy to the input distribution of the visual stimuli maximizes the sensory information encoded and transmitted by the neuron [Laughlin, 1981]. Efficiency in neural coding of visual stimuli has also been observed in vertebrates - from individual neurons in the cat lateral geniculate nucleus (LGN) [Reinagel and Reid, 2000]. As described earlier in Chapter 4, Laughlin [1994] proposed a coding strategy that involves adaptation of the neuronal input-output response relationship. The adaptation of the neural code to the distribution of the input image velocity has been shown to occur at multiple time scales (between tens of milliseconds to a few minutes) [Berry et al., 1997, van Steveninck et al., 1996, Brenner et al., 2000, Fairhall et al., 2001]. Furthermore, such an adaptive neural coding strategy has been shown to maximize the information transmission between consecutive stages of the visuomotor pathway [Brenner et al., 2000, Wainwright 1999].

Brenner et al. [2000] have previously shown the adaptive re-scaling properties of the H1-cell and its role in maximizing information transmission. The authors showed that the input-output (stimulus-response) relationship of the H1-cell scales
in proportion to the standard deviation, $\sigma_v$, of the stimulus velocity distribution. In their study, electrophysiological recordings were made from the H1-cell in *Calliphora* while a vertically oriented grating was presented to the fly. The horizontal velocity of the grating was drawn from a normal distribution with zero mean, $\mu_v = 0$, while the standard deviation, $\sigma_v$, was used as a control parameter. Fig 5.1a shows the spiking rate of the H1-cell along with a stimulus ensemble drawn from a velocity distribution with $\sigma_v = 2.3^o/s$. The ensemble was repeatedly presented to the fly while H1 recordings were made. The corresponding relationship between the horizontal velocity of the grating and the spiking rate of the H1-cell has an approximately sigmoid shape (Fig 5.1b).

The study showed that the sigmoid relationship between the stimulus velocity and the spiking rate of the H1-cell scales in proportion to the standard deviation, $\sigma_v$, of the velocity distribution. Fig 5.2a shows the velocity vs. spiking rate relationship for two stimulus ensembles with $\sigma_v = 2.3^o & 4.6^o/s$. The slight differences between the curves for $\sigma_v = 2.3^o & 4.6^o/s$ disappear if the stimulus velocity is normalized by the standard deviation, $\sigma_v$, and the spiking rate is normalized by the mean spiking rate (Fig 5.2b). Such a re-scaling mechanism allows for the neuron to adapt its response properties to a wider range of stimulus velocity distributions.

The work on the adaptive re-scaling properties of H1 [Brenner et al., 2000] and the corresponding time-scales of adaptation [Fairhall et al., 2001] builds upon the earlier work by [Laughlin, 1981]. However, all these studies were based on neural recordings performed under open-loop conditions. So far only Warzecha and Egelhaaf [1996] studied closed-loop H1 responses, although their analysis did not focus on the adaptive re-scaling properties of the neuron. In this chapter, experiments were performed with the fly-robot interface to measure the neural activity of the H1-cell under closed-loop conditions and the resulting responses were analysed in the context of the neuron’s adaptive re-scaling properties.
Figure 5.2.: Adaptive re-scaling property of the H1-cell. (a) The responses of an H1-cell were obtained for two stimulus ensembles with standard deviation $\sigma = 2.3^\circ/s$ & $4.6^\circ/s$ and plotted against the stimulus velocity. The peak spiking rate for the stimulus ensemble with standard deviation $\sigma = 4.6^\circ/s$ was slightly higher than that with standard deviation $\sigma = 2.3^\circ/s$. (b) Normalizing the spiking rate by the mean spiking rate and the stimulus velocity by the standard deviation of the velocity distribution causes the differences between H1 responses to the two stimulus ensembles to disappear. From [Brenner et al., 2000]

5.2. Experimental Methods

As described in chapters 3 and 4, the proportional and adaptive controllers were used to close the loop in the fly-robot interface. As in the previous chapter different controller gains $K_p = [0.01, 0.1, 0.5, 1.0]$ were tested for the proportional controller and the time windows within which the maximum spike rate was determined for the adaptive controller were set to $\Delta T_{ws} = [0.05, 0.10, 0.15]$ s.

The blowfly was prepared for electrophysiology recordings and the closed-loop responses of the H1-cell in the left lobula plate of the fly were recorded (cf. Section 2.1.4, chapter 2). The responses of the H1-cell were used with a feedback controller to generate compensatory rotations of the robot under closed-loop conditions. The closed-loop H1 responses were logged and used for offline analysis. A systems analysis of the H1-cell response properties was carried out by comparing the moments, i.e. the mean and standard deviation, of the visual stimulus dimensions (cell input) and the H1 spiking rate (cell output). The visual stimulus used for the closed-loop experiments had a fixed contrast and spatial wavelength (Spatial wave-
length $\lambda_{sp} = 11^\circ$, contrast $\approx 100\%$). The only free parameter of the visual stimulus was the horizontal slip-speed which was determined by means of optic flow estimation methods (cf. Section 2.2.2, this chapter). The H1-cell spikes were extracted, by using an amplitude threshold, and convolved with a causal half-Gaussian filter ($\sigma_{fr} = 50$ ms) to estimate the cell’s instantaneous spiking rate.

**Stimulus velocity distribution vs spiking rate**

A proportional controller with controller gain $K_p$ was used to determine the relationship between the variance of the stimulus velocity distribution and the H1 spiking rate under closed-loop conditions. A step response stimulus was delivered by the turn-table and the H1 spiking rates were logged for controller gains $K_p = [0.01, 0.1, 0.5, 1.0]$ ($N = 5$ flies for $K_p = [0.01, 0.1, 0.5]$ and $N = 7$ flies for $K_p = 1.0$). The step stimulus was defined as:

$$\omega_p = \begin{cases} 
0 & \text{for } t < 2.5 \text{ s}, \\
144 \text{ deg/s} & \text{for } t \geq 2.5 \text{ s},
\end{cases}$$

To quantify the relationship between the stimulus velocity and the H1 spiking rate, a sigmoid function was fit to the data in the least-square sense. The sigmoid function was given by:

$$F = \frac{A}{1 + e^{-\beta t}}$$

where, $A$ gives the upper asymptote and $\beta$ describes the growth parameter which determines the slope of the function.

**Bode magnitude and phase plots**

The adaptive controller ($\Delta T_{ws} = [0.05, 0.10, 0.15]$ s) was used to determine the input-output gain and phase relationship for the H1-cell. To obtain the frequency response of the H1-cell for both controllers the stimulus velocity was sinusoidally modulated at different frequencies. The stimulus function with a DC-offset deliv-
The coherence measure was used to quantify the relationship between the stimulus and response as given by (see van Hateren et al. [2005], Theunissen et al. [1996]):

$$C = \frac{\|P_{xy}\|^2}{P_{xx}P_{yy}}$$

where $P_{xy}$ is the cross spectral density of the stimulus and response, $P_{xx}$ and $P_{yy}$ are the power spectral densities of the stimulus and the response respectively.

The results with the adaptive controller were used to determine the coherence at each of the input frequencies $f_i$. For each input frequency, coherence was calculated between the image velocity (stimulus) and the H1 spiking rate (response) for each value of $\Delta T_w$. The mean coherence at each input frequency, $f_i$, was obtained by averaging over all $\Delta T_w$. The power spectral densities, $P_{xx}$ and $P_{yy}$, were estimate using a periodogram, where the stimulus velocity and spiking rate vectors were divided into equal overlapping sections of window length 1 s using a Hamming window of that length in order to prevent spectral leakage.

## 5.3. Adaptive re-scaling in closed-loop

In Fig 5.3, the spiking rate of an H1-cell in closed-loop is plotted against the observed stimulus velocity. As shown by Brenner et al. [2000], the input-output relationship for the H1-cell can be approximated by a sigmoid function (Fig 5.3a). The variability of the cell’s closed-loop responses is much larger than those observed with the cell in open loop (Fig 5.1b). The highly variable responses were possibly due to the non-stationarity of the stimulus velocity distribution under closed-loop
Figure 5.3.: (a) Relationship between slip-speed and spiking rate under closed-loop conditions (blue) and least-squares sigmoid fit ($A = 2.68, \beta = 0.29$) to the data (red) (b) Distribution of slip-speed observed in closed-loop. Data for (a) and (b) were obtained from the fly-robot response with the proportional controller ($K_p = 0.1$) and sinusoidal input ($f_i = 0.03$ Hz).

conditions. The stimulus velocities used by Brenner et al. [2000] and Fairhall et al. [2001] were generated from a normal distribution with zero mean, $\mu_v = 0$ and fixed standard deviation, $\sigma_v$. Under open-loop conditions, the stimulus velocities drawn from such a distribution remains stationary i.e. the standard deviation, $\sigma_v$, of the stimulus velocities remains constant throughout the experiment. While the overall stimulus velocities in closed-loop are normally distributed (Fig 5.3b), the stationarity of the velocities cannot be maintained.

As mentioned earlier, the closed-loop response of the H1-cell to the stimulus velocity can be modeled by a sigmoid function (Fig 5.3a). This function is described by the two fitting parameters $A$ and $\beta$. $A$ is the upper asymptote and represents the (normalized) maximum of the observed spiking rates for the cell. The larger the value of $A$, the larger the peak spiking rate observed by the cell for the given stimulus velocity distribution and vice versa.

The growth factor $\beta$ determines the slope of the sigmoid curve and defines the scaling relationship between the velocity distribution and the H1 spiking rate. $\beta$ is homologous to the scaling factor $\lambda$ introduced by Brenner et al. [2000] and varies to account for the standard deviation, $\sigma_v$, of the velocity distribution. The growth
factor $\beta$ should therefore be low when $\sigma_v$ is large and high when $\sigma_v$ is small.

5.3.1. Effect of the moments of the stimulus velocity distribution on the H1 response function

In order to characterize the H1-cell response under closed-loop conditions, it is important to understand the statistical properties of the stimulus velocity (slip-speed) distribution. The stimulus velocity distribution observed in closed-loop can be described by its first (mean - $\mu_v$) and second (standard deviation - $\sigma_v$) moments. The effects of $\mu_v$ and $\sigma_v$ on the H1 response function, specifically on $A$ and $\beta$, were investigated using the fly-robot interface. A proportional controller with controller
gain $K_p$ was used to provide closed-loop feedback control (cf. chapter 3 for controller description). A step velocity input was provided by the turn-table and the corresponding H1 spiking rate was recorded while the robot compensated for the imposed rotation. The stimulus velocities observed by the fly and the H1 spiking rates were recorded for four different controller gains $K_p = [0.01, 0.1, 0.5, 1.0]$. Gaussian functions were fitted to the stimulus velocity distributions (as shown in Fig 5.3b) and the estimated mean, $\mu_v$, and standard deviations, $\sigma_v$, are shown in Fig 5.4. Both the mean, $\mu_v$, and the standard deviation, $\sigma_v$, increase with increasing $K_p$ (Fig 5.4). Additionally, increasing the mean, $\mu_v$, and the standard deviation, $\sigma_v$, also increases the peak velocity observed by the fly. Increasing $K_p$ for a proportional controller increases the asymmetry in the mean error during closed-loop compensation (cf. results with step input from Chapter 3). This in turn shifts the mean, $\mu_v$, of the stimulus velocity distribution and leads to a larger $\mu_v$ for increasing $K_p$. The mean, $\mu_v$, and standard deviation, $\sigma_v$, are significantly different for low and high values of $K_p$ (Tab ??).

The response of the H1-cell can be parameterized by fitting a sigmoid curve to the H1 response function (for example see Fig 5.3a) for all $K_p$. Prior to fitting, the H1 spiking rate was normalized by the mean spiking rate of the cell in order to account for the inter-individual variance in spiking rates observed across flies. The
relationships between $K_p$ and the fitting parameters $A$ and $\beta$ are shown in Fig 5.5 and further described in Tab ???. Since increasing $K_p$ increases both the mean, $\mu_v$, and the standard deviation, $\sigma_v$ (Fig 5.4), it is not obvious which moment of the velocity distribution impacts on $A$ and $\beta$.

The effect of the standard deviation, $\sigma_v$, on the H1-cell response is straightforward to characterize. As mentioned earlier, open-loop measurements have shown that the H1 input-output function expands or compresses along the x-axis to account for the standard deviation of the stimulus velocity distribution [Brenner et al., 2000, Fairhall et al. 2001]. If the open-loop predictions also hold true in closed-loop, scaling the H1-cell response to the standard deviation, $\sigma_v$, should remove differences between the fitted values of $\beta$ for different values of $K_p$.

To confirm this, the stimulus velocities used to obtained the fits in Fig 5.5 were normalized by $\sigma_v$ and sigmoid curves were fitting to the normalized response functions as before. Note that the responses of the H1-cell had already been normalized by the mean spiking rate of the cell to account for the variability across flies. The fitting parameters of the sigmoid, $A$ and $\beta$, for the normalized response functions are plotting against $K_p$ in Fig 5.6. As predicted by open-loop results, normalizing the H1 response functions by $\sigma_v$ removes the differences between values of $\beta$ for different values of $K_p$.

Note that normalizing by $\sigma_v$ does not affect the relationship between $K_p$ and the asymptote $A$ (Fig 5.5a). This suggests that the peak spiking rate of the H1-cell may be controlled by a moment of the stimulus velocity distribution other than its standard deviation, $\sigma_v$, possibly its mean, $\mu_v$. Furthermore, open-loop experiments on the H1-cell have shown that increasing either the mean, $\mu_v$, [Reisenman et al. 2003] or the standard deviation, $\sigma_v$, [Borst et al. 2005] of the image velocity results in a decrease of its peak spike rate. In our closed-loop experiments, an approximate 2-fold increase in the standard deviation (from $\sigma_v = 16.0$ deg/s to $\sigma_v = 28.5$ deg/s) results in a spike rate reduction of about 18%. Such a decrease is larger than would be predicted for an increased standard deviation under open-loop conditions [Borst et al. 2005]. This suggests that the peak spike rate of the H1-cell under closed-loop conditions depends on both the mean and the standard deviation of the image velocity.
The results in this section show, that the open- and closed-loop responses properties of the H1-cell are similar, in that the response function of the H1-cell is dynamically re-scaled to match the standard deviation of the stimulus velocity distribution. Furthermore, the results suggest that the H1-cell may provide an estimate of the mean of the stimulus velocity distribution by adjusting its peak spiking rate under closed-loop conditions.

5.4. Closed-loop H1 frequency response function

While measuring the H1 response, using image velocities with a step profile, provides useful information about the cell’s response properties, under natural conditions the H1-cell experiences a wide range of yaw velocities and frequencies. The closed-loop response of the H1-cell to a range of dynamic stimuli can be assessed by the cell’s frequency response function. Sinusoidally modulated angular velocities, $\omega_p$, with frequency $f_i = [0.03, 0.1, 0.3, 0.6, 1.0]$ Hz were delivered by the turn-table while the robot compensated for the imposed rotations with angular velocity, $\omega_r$. For the sinusoidal input signals, the peak amplitude was kept con-
stant while the frequency was modulated. The corresponding closed-loop stimulus velocities (H1 input) and spiking rates (H1 output) were recorded for the adaptive controller. The closed-loop stimulus velocities and the H1 spiking rates were converted into the frequency domain and the gain and phase values for each of the input frequencies $f_i$ were calculated.

The Bode gain and phase plots for the closed-loop H1 input-output relationship are shown in Fig 5.7. For all $\Delta T_{ws}$, the H1 response gain decreases linearly over the frequency range tested (Fig 5.7a). The corresponding phase curves were close to zero for the frequency range tested (Fig 5.7b). The phase measurements were noisy around the zero value which slightly skewed the average phase curves in the positive direction. Nonetheless, the variability in the individual phase responses was very low with the phase curves decreasing from approximately $35^\circ$ for $f_i = 0.03$ Hz to around $0^\circ$ for $f_i > 0.03$ Hz.

From the Bode gain and phase plots, a couple of observations regarding the cell’s response properties in closed-loop can be made. The response of the H1-cell decreases at a rate of approximately 8-9 dB/dec with increasing frequency of the image motion under closed-loop conditions. By using sinusoidally modulated velocity stimuli, the responses of the H1-cell to higher order moments of the velocity distribution, i.e. acceleration, can be characterized. Open-loop measurements of the H1-cell have shown that the cell’s responses are sensitive to both the standard
deviation, $\sigma_v$, and the time constant, $\tau$ of the autocorrelation of the stimulus velocity [Borst et al., 2005]. It is important to understand the effect of both $\sigma_v$ and $\tau$ on the stimulus velocity profiles in order to correctly interpret the frequency dependent decrease in gain for the H1-cell.

Increasing $\sigma_v$ increases the amplitude of the stimulus velocity fluctuations. Open- and closed-loop measurements of the H1-cell show that increasing $\sigma_v$ decreases the peak spiking rate of the cell (cf. Effect of the moments of the stimulus velocity distribution on the H1 response function, this Chapter). Fig 5.8 shows the effect on increasing frequency on the stimulus velocity distribution moments. As the frequency increases, the mean remains roughly constant between $-5^\circ - 0^\circ/s$, the standard deviation monotonically increases from around $28^\circ - 46^\circ/s$ while the peak velocities vary between $84^\circ - 122^\circ$. The approximate 1.5 fold increase in the standard deviation, $\sigma_v$, between $f_i = 0.03$ and 1.0 Hz acts to decrease the peak spiking rate of the cell over the tested frequency range (Fig 5.8b). As the mean, $\mu_v$, is roughly constant around 0, its predicted effect on the peak spiking rate will be negligible.

In comparison to the standard deviation, $\sigma_v$, the autocorrelation time constant $\tau$ relates to the periodicity of the stimulus velocity profile in closed-loop. For a sine
wave, the time constant \( \tau \) is equivalent to the period of the function, and in the case of the sinusoidally modulated input stimulus, it is equivalent to the input frequency \( f_i \) (see Eq 5.1). Put another way, increasing the time constant \( \tau \) was equivalent to increasing the input frequency, \( f_i \), of the sinusoidally modulated stimulus velocities. What the H1-cell responds to in closed-loop, however, is a function of both the input sinusoidal velocities and the compensatory response of the FRI. To confirm whether the time constants \( \tau \) or equivalently the input frequencies, \( f_i \), are preserved, the power of the stimulus velocities as observed by the fly in closed-loop were calculated. Fig 5.9 confirms that there is sufficient power (> 4 dB) in order to visually stimulate the H1-cell at that input frequency.

![Figure 5.9](image-url)

**Figure 5.9.: The gain at each of the input frequencies \( f_i \) for the adaptive controller. For all \( \Delta T_w \), the power at the stimulation frequency, \( f_i \), increases linearly with increasing frequency.**

Considered together, both the standard deviation, \( \sigma_v \), and the time constant, \( \tau \), are parameters which affect the acceleration of the stimulus velocities in closed-loop. While increasing \( \tau \) is equivalent to increasing the input frequency, increasing \( \sigma_v \) has the effect of increasing the stimulus velocity amplitudes, both directly increasing the acceleration of the stimulus velocities. The Bode gain (Fig 5.7) for the H1 response function is therefore equivalent to the relationship between the H1 response and the acceleration of the stimulus velocity. Hence, for increasing image acceleration, the gain of the H1-cell decreases linearly at a rate of 8-9 dB/dec under closed-loop conditions. In comparison, while the H1 gain decreases for increasing acceleration, the phase remains constant close to zero over the range of input frequencies tested. Finally, the results suggest that the H1 as a visual sensor
within the optomotor control loop is stable because it does not introduce a phase lag exceeding $-180^\circ$ for gains greater than unity [Ogata 1997].

To summarize, the results from the chapter show that the input-output function scales in proportion to the standard deviation of the stimulus velocity distribution. Also, the results seem to suggest that the H1-cell might encode for the mean of the stimulus velocity distribution. Finally, the responses of the H1-cell were shown to be linearly dependent on the acceleration of the stimulus velocities.

### 5.5. Discussion

Are the response properties of the LPTCs different under open- and closed-loop conditions? While the responses of the H1-cell have been studied extensive under open-loop conditions (e.g. [Brenner et al. 2000], [Borst 2003], [Maddess and Laughlin 1985], [Reisenman et al. 2003]), the results in this chapter represent the first attempt to study the response properties of the H1-cell for a variety of stimulus velocity profiles under closed-loop conditions. The FRI described in Chapter 2 was used to generate dynamical visual stimuli, i.e. sinusoidal and step velocity profiles of the image, and the corresponding H1-cell responses were measured. The only other study where closed-loop electrophysiology recordings were obtained from LPTC’s was carried out by [Warzecha and Egelhaaf 1996]. In that study, electrophysiology recordings were made, under closed-loop conditions, from both the ipsi- and the contra-lateral H1 LPTCs while an immobilized fly was visually stimulated with a grating generated on a CRT display. The differential activity of both H1-cells was used to control the image velocity on the CRT display. A small constant motion bias was introduced into the closed-loop system and the performance of the "computer-neural hybrid" in compensating for the motion bias was tested for different controller gains. The study by [Warzecha and Egelhaaf 1996], however, was limited in two ways. Firstly, they used very small velocities (18°/s) to test the performance of the two H1-cells in compensating for image motion. Secondly, the use of a constant motion bias meant that there was little or no modulation of the acceleration of slip-speeds observed by the H1-cells. In contrast to the dynamic visual stimuli generated by the FRI, the limitations of the experi-
mental protocol used by Warzecha and Egelhaaf [1996] meant that they could not characterize the closed-loop responses of H1-cells for a variety of stimulus velocity profiles. In comparison, one limitation of the FRI is that only the activity of one H1-cell is used for closed-loop control as opposed to both the ipsi and contra-lateral H1 LTPCs. During walking and free-flight, a fly receives information about its yaw rotation from both the ipsi- and the contra-lateral H1’s. Using only a single H1 for closed-loop visual stabilization, would reduce the fly’s sensitivity to measuring yaw rotation on the contra-lateral side. Given that the peak spiking rate of the H1-cell has been found to decrease strongly with an increase in the mean of the velocity distribution, in both open- [Reisenman et al., 2003] and closed-loop (Fig 5.5a) measurements, one key function of two H1-cell’s could be to keep the fly in optomotor equilibrium by trying to minimize the mean velocity of the image motion. In stabilizing for the mean image motion, the fly would remain sensitive to stimulus differences as opposed to absolute values [Taylor and Krapp, 2007]. In the case of the FRI, while using only one H1 certainly reduces the behavioural performance of the FRI in terms of image stabilization (cf. Discussion, Chapter 3), the results in this chapter focus on the neural response properties of the H1 under closed-loop conditions. Therefore, for the reasons outlined above, the H1-cell responses under closed-loop can be reliably characterized using the FRI for a variety of stimulus motion parameters.

The results from this chapter show that the open- and closed-loop responses of the H1-cell to the standard deviation of the stimulus velocity distributions are very similar (Fig 5.3a). By scaling its input-output relationship, the H1-cell maximizes the information transmission between its input and output [Brenner et al., 2000]. However, Fig 5.10 shows that as the standard deviation of the velocity distribution increases, the sensitivity of the H1-cell to pattern accelerations decreases. The sensitivity to acceleration of the H1-cell is also reflected in Fig 5.7a where it decreases at a rate of 8-9 dB/dec for increasing \( \sigma_v \) and autocorrelation time constant \( \tau \). Note, that the acceleration sensitivity of the H1-cell, while changing based on the stimulus velocity distribution, remains highest for when there is little or no pattern motion (\( \sigma_v = 0 \) deg/s, Fig 5.10b). This is clearly advantageous for the fly, as the H1-cell can react quickly and precisely to image motion which rapidly changes direction from the ND to the PD of the cell [Lewen et al., 2001]. It is nonetheless in-
teresting, that the same adaptive re-scaling property that maximizes the information transmission for the cell, comes at a direct cost i.e. that it decreases the H1-cell’s sensitivity to image acceleration. This choice between maximizing either the information transmission or the sensitivity to acceleration might be a design strategy preferred during the evolution of sensory systems. While a decreased sensitivity to acceleration in the visual system might be, in part, compensated by integrating signals from other sensory modalities (i.e. the halteres), a decrease in the information transmission would increase the inefficiencies in the neural representation of motion. Given that neurons are required to process information under very strict energy constraints [Laughlin, 2001] [Laughlin et al., 1998], inefficiencies in neural coding might come at a very high evolutionary cost to the animal. In addition, any inefficiencies in the representation of information at the sensory system level, will propagate downstream and pose problems in control. Therefore, a loss of acceleration sensitivity as a result of the adaptive re-scaling property might be a small cost to pay.

Not only are the responses of the H1-cell to the standard deviation, $\sigma_v$, similar under both open- and closed-loop conditions, the corresponding dependence of the H1 transfer function on acceleration is entirely consistent with open-loop studies. By using reverse correlation techniques, [Brenner et al. 2000] showed that the H1 cell responds to both the velocity and acceleration of the image under open-loop conditions. In addition, under open-loop conditions, the gain of the input-output mapping of the H1 cell was proposed to depend on both the acceleration and the higher-order time derivative of the image velocity profile [Borst et al., 2005] [Borst, 2003].

When considering the similarity of the H1 responses under open- and closed-loop conditions, it is important to consider a few methodological issues. Firstly, that the response properties of the H1 cell, specifically its linear dependence on acceleration is not the result of limitations imposed by the dynamical properties of the robot or the turn-table. The decrease in gain of the input-output function of H1 is too large (8 – 9 Hz), even for small changes in acceleration (between 0.03 – 0.3 Hz) to be explained by the transfer functions of either the robot of the turn-table (cf. Chapter 2). Secondly, in open-loop experiments the image velocity distribution is typically
Figure 5.10: Effect of $\sigma_v$ on the acceleration sensitivity of H1. The fitted values of $\beta$ for the proportional controller with gain $K_p$ are plotted against the standard deviation of the velocity distribution, $\sigma_v$. (a) Increasing $\sigma_v$ linearly decreases $\beta$ as per the relationship specified by the regression line. (b) The normalized input-output functions for three different values of $\beta$ show that (c) decreasing $\beta$ linearly decreases the gradient i.e. the sensitivity of the H1 input-output function at the point $\sigma_v = 0$ deg/s. The results show that increasing $\sigma_v$ directly decreases the acceleration sensitivity of the H1-cell.

kept constant for the duration of the trial (e.g. Brenner et al. [2000], Fairhall et al. [2001]). In such experiments, the stationarity of the image velocity distribution, as characterized by the mean and standard deviation of the image velocity distribution, is assumed to be constant for the whole duration of the H1-cell recording. However, under closed-loop conditions, the image velocity distribution changes during the
course of the trial (Fig 5.3, Tab ??). Even though the stimulus input distributions are completely different across trials, the responses of the H1-cell in closed-loop with dynamic stimuli resemble those measured under open loop conditions.

It is by no means trivial that the response properties of the H1-cell, as characterized by the responses to the moments of the stimulus velocity distribution (mean, standard deviation, acceleration), are highly similar under both open- and closed-loop conditions. It seems to indicate that regardless of whether the fly is compensating for image motion, the neural responses seem to be operating as under open-loop conditions. This agreement between open- and closed-loop responses falls within the sensory paradigm proposed by Warzecha and Egelhaaf [1996] and Borst [2003], in which the nonlinear response properties of the LPTCs can be predicted by the properties of the Reichardt EMD model itself. Warzecha and Egelhaaf [1996] showed that the decrease in H1 gain for increased image velocities was explained by the properties of the motion response properties of the EMDs. Similarly, Borst [2003] showed that an EMD model can explain the dependence of the H1-cell response to the standard deviation and the autocorrelation time constant of the input stimulus velocities. In both cases, no additional feedback signals were required to explain the nonlinear properties of the H1-cell, which were argued to simply be the by-product of the architecture of the early visual system. This paradigm for sensory processing is closely linked to that proposed by Wehner [1987] which argues that the architecture and functional response properties of invertebrate sensory systems reflect a detailed model of the real world. If the model is true, no feedback signals are necessary and the H1-cell responses under closed-loop are simply the result of the EMD response properties, as under open-loop control. A second paradigm for sensori-motor control is that forward model is responsible for modulating the activity of the sensory system based on a copy of the motor output (efference copy) generated by the fly Wolpert and Ghahramani [2000], Krapp and Wicklein [2008], rev: Webb [2004]). Forward models or efference copies have been proposed to explain the mechanism by which flies adjust their gain parameters when faced with unexpected visual feedback during an optomotor task inside a flight simulator. One possible explanation for why the responses of the H1-cell are similar under open- and closed-loop conditions is that no efference copy signal is received at the LPTC level from the motor system. It is crucial to point out, however, that it is not pos-
sible to determine the impact of an efference copy signal by using the FRI. Even though the fly is under closed-loop conditions, it is immobilized for the purpose of obtaining electrophysiology recordings and therefore no motor activity is generated by the flight motor system. It is unsure whether an efference copy is generated even when an animal is not moving, although no effects of it are observable using the FRI. At this point, it is therefore not possible to comment on which control model best explains the fact that the similarity in H1-cell responses as measured under open- and closed-loop conditions.

Finally, within the context of optomotor control, the frequency response function of the H1-cell (Fig 5.7) imposes certain restrictions on fly’s ability to compensate for externally imposed yaw rotations. For the visual system to contribute towards the stabilization of visual motion, the gain attenuation and cut-off frequency of the horizontal cells in the Lobula Plate must be higher than those of the flight muscles which produce the compensatory torque. As discussed in Chapter 1, the response delay in the motion vision pathway (≈ 30 ms) for the fly is very long when compared to other sensory systems like the ocelli (≈ 15 ms) and the halteres (≈ 10 ms). It would therefore make sense that the H1 response function should not have a high gain for high frequencies as this would result in instabilities in the control system. As a result, the cell’s primary function might mainly be to compensate for slow drifts [Collet et al., 1993]. In comparison, the halteres and the ocelli, with their shorted response times, would be better suited to deal with the higher dynamic range. The importance of keeping delays to a minimum within the optomotor control loop is also evidenced by the fact that the H1-cell keeps the phase, or response lag, close to zero over the tested frequency range. A low phase is essential for ensuring that the cell responds immediately to any visual motion and that any control delays do not propagate into the visual stabilization control system downstream from the H1 cell [Dickson et al., 2010].
6. Concluding Remarks

In this chapter I will summarize and discuss work that has been presented earlier in my thesis. The contributions of the individual chapters are discussed in the context of the original motivation for the work. Finally, I will outline advances made and possible future research directions which can be explored based on my work.

6.1. Summary

The work presented in this thesis falls within a larger goal of understanding the neural mechanisms involved in the multisensory integration of information under closed-loop conditions. In order to obtain a true picture of how an animal transduces, combines and processes sensory information in order to produce movement requires that the neural and the behavioural activity be measured simultaneously as the animal interacts naturally with the environment. The problem of studying the neuronal principles underlying multisensory integration can be made simpler by studying it in a model system which has a neural system and architecture which is a few orders of magnitude simpler. Furthermore, the problem can be made simpler yet by limiting the behaviour in the model system to inner-loop stabilization reflexes.

In the research presented in Chapters 2-5, I tackled a small subset of the general problem described above relating to the neuronal mechanisms underlying multisensory control. Specifically, the aim of this thesis was to study the neural strategies underlying visuo-motor control using the fly as a model system. The contributions
of each of these chapters towards the aims of the thesis are summarized below.

In Chapter 2, I present a novel experimental system that I built and tested in order to study the neural strategies underlying inner-loop visuo-motor control in the fly. The experimental system consisted of a fly-robot interface (FRI), where the neural activity from an identified visual interneuron, the H1-cell, was used to control the counter-rotation of a mobile robot placed on a rotating turn-table (Fig 2.1). High-speed images captured by two cameras mounted on the robot were transmitted and displayed on two CRT monitors placed in front of the fly. Electrophysiology recordings were made from the left H1 cell and the resulting spiking activity was used to control the rotation of the robot. Both the robot and the turn-table were constrained to rotate along the horizontal plane, therefore constraining the fly to perform an image stabilization task along 1 DoF i.e. the optomotor response. The FRI was designed such that different control laws could be used to close the loop between the neural activity of the H1 cell and the rotation of the robot.

In Chapter 3, I used a simple proportional controller to investigate the performance of the FRI for the optomotor task (Fig 4.2b). I used a control theoretic approach to characterize the performance of the FRI under closed-loop conditions. Specifically, I used the step response, frequency response and optimal function to characterize the FRI performance. The FRI along with the proportional controller was a proof of concept that the fly can use its neural activity to stabilize visual motion in closed-loop. I found that for low values of the controller gain, the FRI was able to compensate well for constant velocity motion (Fig 3.6b). However, high controller gain, I found significant control oscillations in the FRI as a result of the natural frequency of the system (Fig 3.6d). Similar unexplained control oscillations were observed in single torque responses measured from a fly during tethered flight [Mayer 1989, Warzecha and Egelhaaf 1996, Wolf and Heisenberg 1990]. Similarly, Harrison and Koch (2000) also observed control oscillations in single torque responses when a silicon implementation of the fly’s optomotor system was used to minimize visual-slip speed under closed-loop conditions. The model of the fly’s HS-cell was implemented as the spatial summation of multiple EMDs, which in turn was low-pass filtered ($\tau = 680$ ms) to mimic the behaviour of the motor system and obtain the torque response. In the absence of any control-loop delays,
Harrison and Koch [2000] reported that the delays associated with the cross-arms of the EMDs ($\tau = 40$ ms) and the motor system ($\tau = 680$ ms) were sufficient to produce these control oscillations. In the light of these results, I propose that the previously unexplained control oscillations observed in optomotor responses measured during tethered flight can possibly be explained as a result of a high controller gain coupled with the natural frequency which results from mounting the fly on a tether [Mayer 1989, Warzecha and Egelhaaf 1996, Wolf and Heisenberg 1990]. The control oscillations as a result of the natural frequency led to a strong resonant/anti-resonant phenomenon in the FRI frequency response (Fig 3.9). Finally, I found that no specific value of the manually adjusted controller gain was able to perform visual stabilization optimally over the tested frequency range (Fig 3.10). From the results, I proposed that the best neural strategy for optomotor control might be to constantly adjust the controller gain based on the angular velocity and acceleration of the visual slip-speed.

Following the predicted strategy in Chapter 3, in Chapter 4 I designed an adaptive gain controller based on the adaptive coding strategy proposed by for maximizing the information capacity in Large Monopolar Cells (Fig 4.5). Although the control oscillations observed with the proportional controller were also observed for the adaptive controller (Fig 4.4), the resonator/anti-resonator phenomenon in the frequency response of the FRI vanished (Fig 4.6). As a consequence of removing the resonator/anti-resonator phenomenon, the adaptive controller increased the frequency response bandwidth for the 1 DoF optomotor task (Fig 4.8). With the results in the chapter, I showed that a neural strategy for optomotor control that used an adaptive gain, was able to maximize the bandwidth for the FRI frequency response, given the constraints imposed by the low-pass filter characteristics of the robot providing the compensatory rotation response.

Finally, in Chapter 5, I quantified the effect of the visual slips-speeds observed by the fly on the response properties of the H1-cell under closed-loop conditions. I found that the open- and closed-loop response properties of the H1-cell were very similar. I found that the closed-loop responses of the H1-cell were highly sensitive to non-zero means of the stimulus velocity distribution (Fig 5.6). I suggest that this is evidence that the ipsi- and contra-lateral H1 system acts to keep the fly in
optomotor equilibrium i.e. no apparent visual motion. Additionally, I found that as with the open-loop responses, the input-output function of the H1-cell scaled in proportion to the standard deviation of the stimulus velocity distribution (Fig 5.6). I present evidence that increasing the standard deviation of the stimulus velocity distribution linearly decreases the sensitivity of the H1-cell to acceleration (Fig 5.7 and Fig 5.10). I report that while the adaptive re-scaling property of the cell serves to maximize the information transmission between the input and output, it comes at a direct cost of decreased sensitivity to acceleration and that the outcome of this trade-off is decided by evolutionary pressures. I also find that the H1-cell keeps delays downstream within the optomotor loop to a minimum by keeping its phase lag around zero (Fig 5.7). In conclusion, I report that there is no evidence that a forward model, or efference copy, is provided or acts to alter the response properties of the H1 cell under closed-loop conditions.

The works presented in Chapters 2-4 have been published in peer-reviewed journals and conference proceedings (cf. Appendix B). The work in Chapter 5 has been accepted for a special call for papers, and the manuscript is currently in preparation.

The key contributions of this thesis are presented in bullet points below:

### 6.1.1. Key Contributions

- Built the FRI for investigating the neuronal strategies underlying optomotor control and provided a proof-of-concept that the neural signals of the H1-cell can be used to control a robotic controller in order to compensate for and stabilize visual motion.
- Found that using the neuronal signals of the H1-cell to control a robotic controller with real-world dynamics results in a natural frequency of the system which gives rise to control oscillations for large controller gains.
- Found that a linear (proportional) neural control strategy was not able to provide optimal visual stabilization performance for the tested input frequencies.
- Proposed and characterized a nonlinear (adaptive gain) neural control strategy that maximizes the bandwidth for the frequency response of the FRI.
• Characterized the closed-loop response properties of the H1-cell and found that increasing the standard deviation of the stimulus velocity distribution linearly decreases the cell’s sensitivity to acceleration.

• Found that the adaptive re-scaling property of the H1-cell responsible for maximizing the information transmission comes at the direct cost of decreased sensitivity to acceleration for the cell.

• Found that the response properties of the H1-cell are highly similar under both open- and closed-loop conditions.

6.2. General Discussion

6.2.1. Reductionist approach to studying neural strategies for visuo-motor control

The larger goal which I try to build up towards is the characterization of the neural dynamics observed while a fly performs a visual stabilization task. For the reasons mentioned in the start of the preceding section, recording neuronal signals and measuring the flight motor activity from an unrestrained freely flying fly remains the goal towards which experimentalists in the field are working towards. While technological and methodological issues such as the excessive size of electrophysiological equipment and limited stability of neural recordings in unrestrained flies are still very challenging, only recent advances in the development of customized micro recording probes may offer a solution to those problems [Peterson, 2011] (also cf. Future Work). Due to the methodological restrictions, one successful approach has been and still is to reduce the complexity of the behavioural task, for instance by tethering a fly to a torque meter and measuring the dynamics of visuo-motor stabilization reflexes along only 1 DoF (*Drosophila melanogaster*: Heisenberg and Wolf [1988], Wolf and Heisenberg [1979], Heisenberg and Wolf [1984]; blowfly *Lucilia*: Warzecha and Egelhaaf [1996], Kern and Egelhaaf [2000]). While previously used experimental setups have yielded extensive insight into how physical torque is generated during an optomotor responses, the question as to how the
so called "neural torque", defined by Heisenberg and Wolf [1993] is used to control the physical torque is still poorly understood and is what I try to address in this thesis.

6.2.2. Robustness of the optomotor response

The inspiration for part of this thesis came from closed-loop behavioural experiments carried out by Wolf et al. [1992]. In the study, Wolf placed a fly inside a cylindrical drum, the walls of which were lined with a single vertically oriented black bar. The fly was fixed in the center of the drum such that it faced the bar and its front legs rested on a small force sensitive lever. In the experiments, the fly was able to use the differential activity of its front legs in order to stabilize the observed visual motion under closed-loop conditions. The fly was still able to perform visual stabilization in this experimental setup even when the polarity of the error signal was inverted. The experiments by Wolf et al. [1992] were evidence that the optomotor reflex in the fly is highly robust, that the fly can use novel feedback configurations in order to stabilize visual motion. However, in the study the neural activity was not used to close the loop between the fly and the visual motion. Instead the fly was able to try out a number of sensori-motor links and use the one that correlated with the image motion. With the FRI, however, different controllers had to be used in order to test out the effect of different neural control strategies on the performance of the FRI in stabilizing the visual motion observed under closed loop. Nonetheless, that the fly was able to use the FRI to compensate for visual motion over the large range of input frequencies tested further demonstrates the versatility of the fly’s visuo-motor system.

6.2.3. Choice of the robot controller for providing real-world dynamics

The experimental system I designed consists of a FRI, where the neural torque i.e. the activity of the H1 LPTC was used to control the physical torque, in this instance the rotation of a mobile robot. One straight-forward approach to coupling
the neural and the physical torque would be to simply use the activity of one or both H1 LPTCs to control the image velocity on a CRT monitor in front of the fly. This is the approach previously used by [Warzecha and Egelhaaf, 1996]. Using a robot however incorporates complex dynamics due to inertia, damping and slippage into the closed-loop compensation responses. These dynamics directly affect the natural frequency of the closed-loop system which, as shown by the results in Chapters 3-5, have a significant effect on both the observed neural and the performance of the FRI. That it was possible to control the rotation of the robot using the H1-cell activity, the dynamics of which are very different from its flight motor system, may not be surprising.

One of the limiting factors in choosing a robot was its ability to carry a significant weight. The fly has a very high flicker fusion frequency [Autrum, 1958], and high-speed cameras are required in order to stimulate its visual system correctly so that the fly observes continuous image motion. Robotic systems exist which have much faster motion dynamics than the ASURO robot I used, such as the 3pi (Polulu Robotics and Electronics), however, they are not capable of carrying the weight payload of the high-speed cameras (92 g each) and the associated battery packs. Using a smaller and lighter robot does however provide the advantage of having a much higher cut-off frequency associated with its frequency response. This would allow for testing the response of the FRI, and the corresponding H1 responses, over a much larger range of frequencies. To summarize, I selected the ASURO robot as a balance between faster dynamics and ability to carry a higher weight payload.

### 6.2.4. Choice of methods for characterizing neural and FRI dynamics

It is worth pointing out, that a number of methods used for characterizing neuronal responses under open-loop conditions cannot, for methodological reasons, be used under closed-loop conditions. For example, reverse correlation techniques are a useful class of methods for quantifying the impulse response function of a cell (cf. [Brenner et al., 2000]) and it would be very useful to derive and compare the impulse functions for the H1 cell under both open- and closed-loop conditions. However, in
order to obtain a meaningful impulse function, the cell needs to be stimulated with an image velocity distribution that contains a large range of frequencies. Under open-loop conditions, a white noise signal is used as the pattern velocity distribution. However, as discussed earlier in Chapter 5, due to the compensatory nature of closed-loop responses, the stimulus velocity distribution changes over the course of a trial. Furthermore, for most cases, the image velocities observed by the fly under closed-loop conditions have strong auto-correlations ($\tau \approx 1$ s, natural frequency of the system). Since the image velocities have such strong temporal correlations, even using pre-whitening techniques do not help in obtaining meaningful impulse functions for the H1 cell under closed-loop conditions. Similarly, another useful comparison to make would be to compare the SNR and the channel capacity of a cell between open- and closed-loop conditions. However, many such information theoretic methods (e.g. SNR, channel capacity, information content) also depend on the use of the same white noise stimulus repeatedly presented to a cell. As white noise cannot be reliably presented to the cell under closed-loop conditions, comparisons between these information theory metrics for the cell cannot be made between open- and closed-loop conditions. In contrast to information theoretic approaches, control theory provides a set of methods that allow for the analysis and characterization of closed-loop control systems. The step response, frequency response and optimal functions used to characterize the performance of the FRI and the response of the H1-cell in chapters 3-5 are all obtained from control theory.

### 6.2.5. Linear versus nonlinear control

In contrast to information theoretic approaches, control theory provides a set of methods that allow for the analysis of closed-loop control systems. One important aspect of closed-loop control that often gets overlooked in flies is the problem of linearity. While optomotor responses in flies have shown to be linear at the behavioural level (Calliphora: Schwyn et al. [2011], Drosophila: Graetzel et al. [2010], also see: Taylor and Krapp [2007]), the corresponding neuronal responses of cells which are involved along the sensori-motor pathway generating these behaviours are highly nonlinear [Reisenman et al., 2003]. In order for the fly to be able to achieve top level linearity, it needs to solve a complicated engineering prob-
A neuronal processing stage is required in order for the nonlinear responses to approximate top-level linearity. With respect to optomotor control, this neuronal processing stage represents how the nonlinear responses of LPTCs i.e. the HSE and HSN, are converted into a command signal to the flight motor system which in turn generates yaw torque as a linear function of the slip-speed. The exact nature of this neuronal processing stage is still an open question.

The only other study on optomotor control which used nonlinear responses of the H1 cell to control image motion, used a linear feedback controller to close the behavioural loop [Warzecha and Egelhaaf, 1996]. While a linear controller is a simple choice for feedback control as a first approximation, it cannot explain how the nonlinear neural signals are converted into top level linear behaviour. A fundamental difference between the two feedback controllers used in chapters 3 (static gain or proportional controller) and 4 (dynamic or adaptive gain controller) is that of linearity. The static and adaptive gain controllers are examples of linear and nonlinear controllers respectively. While there are many different forms of linear and nonlinear feedback controllers, the results presented in Chapter 3 and 4 represent the first study to quantify and differentiate between the performances of the two categories within the context of optomotor control. One key finding that I report here is that the adaptive gain controller is able to minimize the disruptive effect of the natural frequency of the system on the optomotor response. Furthermore, the performance of the adaptive gain controller in minimizing visual slip-speed is comparable to that of the static gain controller. Additional control parameters which indicate the performance of the controller, i.e. phase differences, rise times and overshoot, are also better for the adaptive as compared to the static gain controller.

The performance differences between the linear static gain- and the nonlinear adaptive gain controllers can possibly help explain the differences in optomotor responses obtained under open- and closed-loop conditions [Heisenberg and Wolf, 1993]. In the study, the authors carried out a series of master-replay experiments, where first they recorded yaw torque generated by a fly in response to sinusoidal image motion under closed-loop conditions (master trace). The resulting slip-speed traces observed by the fly were recorded and subsequently played back to the same fly under open-loop conditions (replay trace). The authors observed that the re-
sponses in closed-loop were considerably larger than those in open-loop. To explain this phenomenon, Kirschfeld [1989] has suggested that an efference copy of the motor output might provide a frequency dependent feedback signal to the optomotor system. Heisenberg and Wolf [1993] argues that the power spectral density for the yaw torque under open- and closed-loop conditions are very similar, and only differ at the low frequencies. Therefore, a frequency dependent feedback signal would therefore have to primarily operate at low frequencies. The combined results of Chapters 4-5 agree with the optomotor model proposed by Heisenberg and Wolf [1993] and Kirschfeld [1989]. The results from Chapter 4 show that the adaptive controller provides a frequency dependent feedback gain to the optomotor control loop. Complementary to that, the H1 frequency response calculated in Chapter 5 shows that the cell is highly responsive for lower frequencies, with the gain reducing linearly with an increase in frequency. Furthermore, the similarity between H1 responses under open- and closed-loop conditions seems to suggest that the frequency dependent efference copy signal does not arrive at the level of the H1-cell. It should be noted, however, that it is not possible to assess the impact of an efference copy signal by using the FRI in its current configuration. Even though the fly is under closed-loop conditions, it is immobilized for the purpose of obtaining stable electrophysiology recordings. In the absence of any motor activity, the effect of an efference copy signal on the H1-cell responses within the FRI is unlikely to be observed. Furthermore, a frequency dependent feedback signal does not necessarily have to be based on an efference copy of the motor output, but could also be the result of (locomotor) state-dependent processing of visual information by the fly LPTCs [Longden and Krapp, 2009, 2010, Jung et al., 2011, Maimon et al., 2010, Chiappe et al., 2010].

6.2.6. Natural frequency of the FRI system

An emergent property of the FRI is the presence of control oscillations as a result of the natural frequency of the closed-loop experimental system. While it is very likely that these control oscillations are the result of the dynamical properties of the robot used in the FRI, similar control oscillations have previously been reported when observing yaw torque fluctuations during tethered flight [Mayer]
Similarly, control oscillations are a common feature of eye movements in most animals (humans: Miles and Wallman [1993], crabs: Sademan [1978], monkeys: Robinson et al. [1986], Goldreich et al. [1992]; for review see Lisberger et al. [1987]). The results of Chapter 3 suggest that these control oscillations might be the result of a high controller gain. As the sensory systems of insects are proposed to measure changes in stimuli and not absolute values [Taylor and Krapp, 2007], these control oscillations might be the natural albeit unwanted by-product of such a differential sensory system. Large amplitude control oscillations, however, are a serious threat to the stability of any control system. Therefore, neural systems through evolution would have found ways of keeping the control oscillation amplitudes bounded within a certain range. One possible mechanism for this was proposed by Warzecha and Egelhaaf [1996], who showed that the intrinsic properties of the EMDs helped reduce the overall gain when control oscillations start building up and the system approaches instability. Another complementary mechanism that is considered to be responsible for control oscillations is latencies within the control loop [Sademan, 1978, Robinson et al., 1986, Goldreich et al., 1992]. Reducing the phase differences upstream in the optomotor pathway, i.e. at the level of the H1 cell, would help prevent instabilities. The results from Chapter 5 show that the closed-loop responses of the cell attempt to keep the phase constant close to zero over a large range of frequencies. By responding very quickly to image motion, the H1 cell is able to reduce any phase delays from propagating downstream along the optomotor pathway therefore reducing the chances of the system becoming unstable.

6.3. Future work

The work presented in this thesis can be primarily extended into the following areas:
Neural control of the optomotor response using both H1 LPTCs

One of the main limitations of the FRI is that its performance has been categorized for only one H1-cell. One obvious improvement would be the use of both H1-cells for closed-loop visual stabilization. One question of interest would be to determine the effect of using two H1 cells on the control oscillations due to the natural frequency of the FRI. Furthermore, using both H1 cells allows for testing a larger range of both linear and nonlinear controllers, especially since the sensitivity to errors resulting from both clockwise and anti-clockwise yaw rotations will now be approximately the same.

It should be noted that the only study to use the activity of both H1 cells reported the difficulty in maintain recording stability for both H1-cells long enough to characterize the system [Warzecha and Egelhaaf, 1996]. In that study, they were only able to record the ipsi- and contra-lateral H1-cells for 2 flies. The experiments with both H1-cells will no doubt be challenging, but are possible given the recent advances in closed-loop electrophysiology [Jung et al., 2011, Maimon et al., 2010, Chiappe et al., 2010].

Optomotor dynamics during tethered flight

One of the predictions from the work presented in Chapter 3 is that the natural frequency of the experimental system combined with a high gain can explain the control oscillations observed in a flight simulator during tethered flight [Mayer, 1989, Warzecha and Egelhaaf, 1996, Wolf and Heisenberg, 1990]. A natural frequency in an experimental system could be induced simply by mounting the fly asymmetrically on the tether.

It is therefore worth considering whether the natural frequencies in optomotor torque meter experiments have potentially had an impact on the results. And if yes, then how much of an impact does the natural frequency have on optomotor dynamics in tethered flight.

By using the control theory methods described in Chapters 3-5 in this thesis, the optomotor dynamics of a fly in tethered flight can be characterized. The step and
frequency response characterizations should give the overall effect of the natural frequencies on the overall optomotor response observed during closed-loop conditions.

**Effect of locomotor state on FRI performance**

One key question is regarding the effects the different locomotor states of an animal has on its performance in minimizing the visual-slip speeds it observes during motion. Recently Chiappe et al. [2010] found that the temporal frequency tuning of the HSN-cell was shifted towards higher values when the fly was walking (3 Hz) versus at rest (1 Hz). Similarly, Jung et al. [2011] reported that the temporal frequency tuning of the H1-cell was also shifted towards higher values when the fly was flying (7 Hz) as compared to being stationary (2 Hz). Both these studies predict that changing the locomotor state of the fly from stationary to walking or flying results in an increase in the temporal tuning function of the visual interneurons to account for the increased slip-speeds observed during motion. This predicts that using neural recordings from flies which are in a locomotor state other than rest for correcting for visual slip-speeds within the FRI would result in an increase in performance for higher temporal frequencies. One way of testing this prediction would be to alter the locomotor state of an immobilized fly by the application of the octopamine agonist chlordimeform (CDM).

CDM is an invertebrate neurotransmitter and its application in immobilized flies has previously been shown to decrease the response latency [Longden and Krapp, 2009] and increase the spontaneous activity of the H2-cell [Longden and Krapp, 2010]. Furthermore, the application of CDM also mimicks the shift in temporal frequency tuning of the H1-cell to higher frequencies observed during flight [Jung et al., 2011]. Therefore, the application of CDM to flies within the FRI could serve as a model system to investigate the performance of the fly in correcting for visual slip-speeds when it is induced into different locomotor states.
Neural strategies underlying lift control

The same analysis and methods used to characterize the neural control strategies underlying optomotor response in this thesis can be expanded to characterize other visually mediated behaviours. Graetzel et al. [2010] used sinusoidally modulated stimulus velocities to characterize the visually mediated lift response in Drosophila and found that the behaviour could be modelled by a linear time-invariant system. The same visually mediated lift response can be characterized in Calliphora using a modified FRI. The robot can be replaced with a helicopter/hovercraft that carries to high-speed video cameras which transmit and display images to a couple of CRT monitors placed in front of the fly. The same linear and nonlinear controllers used in Chapters 3 and 4 can be used to close the loop between the lift response and the cells in the vertical system of the LPTCs and the neural response properties and performance of the FRI characterized in much the same way as the optomotor response in this thesis.

Nonlinear neuro-prosthetic control

The nonlinear adaptive gain controller can be used as an inspiration for designing and testing the next generation of neuro-prostheses. One fundamental problem with implanted multi-electrode arrays (MEAs) is that scar tissue degrades signal quality over time. A nonlinear controller could be designed to adapt the feedback controller gain based on the evolving SNR from the MEA.

Multisensory control in the fly

As mentioned at the start of this chapter, the work in this thesis is part of a larger effort to develop the technology and methods to study multi-sensory control in an unrestrained/minimally restrained fly. In recent work, Peterson [2011] has developed a micro-recording probe (MRP) for measuring the neuronal activity in a minimally restrained fly (Fig 6.1). The MRP is designed to be inserted into the back of the fly’s head, where it will use four electrodes to record from LPTCs. The
fly can then be placed onto a mobile robot while neural recordings are made from it. As the robot moves through space, the fly will receive multisensory feedback regarding its self motion. The fly-on-a-robot experimental setup can therefore be used to study the relative contributions of the individual sensory systems at the neuronal level. This would be possible by measuring the neural activity with the fly on the robot and all its sensory modalities intact, and then comparing it to when the sensory modalities are individually disabled. In case the chip allows for measuring the neural activity in an intact fly during tethered flight, even the contributions of efference copies on the closed-loop responses of the LPTCs can be assessed.

Figure 6.1.: (a) The micro-recording probe shown inside its packaging (Image from Peter-son [2011]).
A. Appendix

A.1. Optic Flow

The problem of estimating optic flow from a set of images can be defined as follows:

**Problem definition:** Find for each pixel \((x, y)\) a velocity vector \(\vec{u} = (u, v)\) which says how quickly the pixel is moving and in which direction.

**Brightness constancy assumption:** assume that image intensity \(I\) at a point \((x, y)\) at time \(t\) is constant. It follows that if after a short time \(\Delta t\), the point moves a short distance \((\Delta x, \Delta y)\), then:

\[
I(x, y, t) = I(x + \Delta x, y + \Delta y, t + \Delta y) \quad \text{(A.1)}
\]

Expanding [A.1] using first-order taylors series:

\[
I(x, y, t) = I(x, y, t) + \frac{\partial I}{\partial x} \cdot \Delta x + \frac{\partial I}{\partial y} \cdot \Delta y + \frac{\partial I}{\partial t} \cdot \Delta t
\]

\[
= I(x, y, t) + I_x \cdot \Delta x + I_y \cdot \Delta y + I_t \cdot \Delta t
\]

\[
0 = I_x \cdot \Delta x + I_y \cdot \Delta y + I_t \cdot \Delta t
\]
Dividing throughout by $\Delta t$:

\[ 0 = I_x \frac{\Delta x}{\Delta t} + I_y \frac{\Delta y}{\Delta t} + I_t \]

\[ -I_t = u \cdot I_x + v \cdot I_y \]  \hspace{1cm} (A.2)

where $u = \frac{\Delta x}{\Delta t}$ and $v = \frac{\Delta y}{\Delta t}$

Equation [A.2] is also referred to as the brightness constancy equation. $I_x, I_y, I_t$ are known from the images. This leaves two unknowns $(u,v)$ to solve for, with only one equation. In $(u,v)$ space, the solution lies along the line:

\[ v = u \cdot \frac{I_x}{I_y} + \frac{I_t}{I_y} \]

Figure A.1.: Solution space for the brightness constancy equation lies along the line $-I_t = \ u \cdot I_x + v \cdot I_y$. The true flow vector $(\dot{u}, \dot{v})$ can be separated into the independent parallel, $p$, and normal, $d$, flow components.

Fig [A.1] shows the solution space for the brightness constancy equation. Assuming $(\dot{u}, \dot{v})$ is the true flow, then it consists of two independent components, the normal flow $d$ and the parallel flow $p$. Typically, only a patch of image is analysed when computing the local motion of an image pixel $(x,y)$. This gives rise to the aperture problem as shown in Fig [A.2]. When trying to estimate the true motion $(\dot{u}, \dot{v})$, the aperture problem only allows for the estimation of the normal flow, $d$ and the
parallel flow, $p$, cannot be calculated.

Figure A.2.: The aperture problem encountered while calculating local motion. A line with fixed intensity at all points is observed to move from its original position at time $T$ to its new position at time $T + \Delta T$. The motion of the line can however only be observed through a small aperture. Reconstructing the motion of any point on the line is ambiguous. Since all points of the line are all equal intensity, any motion of a point along the line (parallel flow $p$) cannot be estimated. Faced with the aperture problem, only the normal flow, $d$, for the motion of the line can be estimated.

Computational methods can be used to resolve the normal local motion $d$. Two of the most popular and widely used computational methods are the Lucas-Kanade \citep{Lucas1981} and The Horn-Schunk \citep{Horn1981} algorithms. While the Lucas-Kanade method analyzes local image motion, the Horn-Schunk analyzes global motion. Both methods have competing benefits and tradeoffs: local methods are typically robust when faced with noise while global methods are able to estimate image flow fields which are dense but are more sensitive to noise \citep{Bruhn2005}. Both the Lucas-Kanade and Horn-Schunk method were used to estimate motion for the grating pattern stimulus used with the fly-robot interface. The best performance was achieved with a variant of the Lucas-Kanade method called the pyramidal Lucas-Kanade \citep{Bouguet2000} which is described in the section below.

**Lucas-Kanade Method**

The Lucas-Kanade method assumes local smoothness, i.e. a constant $(u, v)$ in a small neighbourhood. For a given set of points in a neighbourhood $[(x_1, y_1),...,
(x_2, y_2 \ldots (x_n, y_n))$, it follows from Eq[A.2]

\[
\begin{bmatrix}
I_{t_1} \\
I_{t_2} \\
\vdots \\
I_{t_n}
\end{bmatrix}
= 
\begin{bmatrix}
x_1 & y_1 \\
x_2 & y_2 \\
\vdots & \vdots \\
x_n & y_n
\end{bmatrix}
\begin{bmatrix}
u \\
v
\end{bmatrix}
\] (A.3)

This allows for formulating the problem as the following energy cost function:

\[
E = \sum (u \cdot I_x + v \cdot I_y + I_t)^2
\] (A.4)

Minimizing[A.4] by equating the partial derivatives to zero:

\[
\frac{\partial E}{\partial u} = \sum 2I_x (u \cdot I_x + v \cdot I_y + I_t) = 0
\]

\[- \sum I_x I_t = u \sum I_x^2 + v \sum I_x I_y \]

\[- \sum I_x I_t = \begin{bmatrix}
\sum I_x^2 & \sum I_x I_y
\end{bmatrix}
\begin{bmatrix}
u \\
v
\end{bmatrix}
\]

And similarly for \( \frac{\partial E}{\partial v} \):

\[
\frac{\partial E}{\partial v} = \sum 2I_y (u \cdot I_x + v \cdot I_y + I_t) = 0
\]

\[- \sum I_y I_t = u \sum I_x I_y + v \sum I_y^2 \]

\[- \sum I_y I_t = \begin{bmatrix}
\sum I_x I_y & \sum I_y^2
\end{bmatrix}
\begin{bmatrix}
u \\
v
\end{bmatrix}
\]

153
combining results from the partial derivatives:

\[
\begin{bmatrix}
-\sum I_x I_t \\
-\sum I_y I_t
\end{bmatrix} =
\begin{bmatrix}
\sum I_x^2 & \sum I_x I_y \\
\sum I_x I_y & \sum I_y^2
\end{bmatrix}
\begin{bmatrix}
u \\
v
\end{bmatrix}
\]

solving for \( \vec{u} \):

\[
\begin{bmatrix}
u \\
v
\end{bmatrix} = \begin{bmatrix}
\sum I_x^2 & \sum I_x I_y \\
\sum I_x I_y & \sum I_y^2
\end{bmatrix}^{-1}
\begin{bmatrix}
-\sum I_x I_t \\
-\sum I_y I_t
\end{bmatrix}
\]

\[
\begin{bmatrix}
u \\
v
\end{bmatrix} = \frac{1}{\sum I_x^2 \sum I_y^2 - (\sum I_x I_y)^2}
\begin{bmatrix}
\sum I_x^2 & -\sum I_x I_y \\
-\sum I_x I_y & \sum I_y^2
\end{bmatrix}
\begin{bmatrix}
-\sum I_x I_t \\
-\sum I_y I_t
\end{bmatrix}
\]

(A.5)

The Lucas-Kanade method solves the brightness constancy equation by solving equation A.5. However, Lucas-Kanade only works given some assumptions.

Firstly the brightness should be constant. Despite some flickering lights in the experimental setup the brightness was mostly constant over the scene captured by the cameras. Secondly, a point should move like its neighbours i.e. there is coherence in motion of the visual scene. This assumption also holds true as the images used in the experimental system consists of the horizontal motion of a vertical grating pattern. Thirdly, both Horn-Shunck and Lucas-Kanade methods only work for slow motion. For fast motion the brightness changes too rapidly to be captured by the taylor expansion. To account for this, multi-scale estimation can be carried out to calculate optic flow at different pixel resolutions. Such a multi-scale version of the Lucas-Kanade method is known as the Pyramidal Lucas-Kanade method [Bouguet, 2000]. The pyramid method works by first down sampling the images to a lower pixel resolution and computing the image motion using the Lucas-Kanade method. The pixel resolution is then increased and the image motion results from the images with lower pixel resolution are used as a seed for the current level. Different numbers of pyramid levels can be used depending on the requirements.

Once the optic flow fields have been calculated from the camera images, the in-
individual vectors in the flow field are projected onto the horizontal unit vector \( \hat{j} \). The sum of all the projection vectors gives the horizontal rotation estimated by the pyramidal Lucas-Kanade method.

### A.2. Derivation for \( F \rightarrow E \)

The nonlinearity used for calculating the slip-speed error \( E \) from the instantaneous firing rate \( F \) is calculated by mapping the input-output range of a cosine curve (see Fig A.3) onto the desired input and output ranges given by:

\[
(F_{\text{spont}}, F_{\text{max}}) \rightarrow (0, E_{\text{max}}) \quad \text{see Fig A.4a}
\]

\[
(0, F_{\text{spont}}) \rightarrow (-E_{\text{min}}, 0) \quad \text{see Fig A.4b} \quad (A.6)
\]

![Figure A.3](image)

**Figure A.3.** Cosine input-output range which is mapped onto the ranges given by Eq A.6
Figure A.4: Nonlinearities used for estimating the slip-speed error $E$ when firing rate $F$ is above and below the spontaneous firing rate $F_{\text{spont}}$. Nonlinear functions are given as (a) $g_{\text{max}}(F)$ & (b) $g_{\text{min}}(F)$.

**Derivation of $g_{\text{max}}(F)$**

Required mapping:

\[
(F_{\text{spont}}, F_{\text{max}}) \rightarrow (0, E_{\text{max}}) \tag{A.7}
\]

Therefore, domain conversion is given by:

\[
-\frac{1}{2} \leq x \leq 0 \quad \rightarrow \quad F_{\text{spont}} \leq F \leq F_{\text{max}}
\]
Which gives,

\[ 0 \leq F - F_{spont} \leq F_{\text{max}} - F_{spont} \]

\[ \Rightarrow 0 \leq \frac{F - F_{spont}}{F_{\text{max}} - F_{spont}} \leq 1 \]

\[ -\frac{1}{2} \leq \frac{1}{2} \left( \frac{F - F_{spont}}{F_{\text{max}} - F_{spont}} - 1 \right) \leq 0 \]

\[ -\frac{1}{2} \leq -\frac{1}{2} \left( \frac{F - F_{\text{max}}}{F_{spont} - F_{\text{max}}} \right) \leq 0 \]

\[ x = -\frac{1}{2} \left( \frac{F - F_{\text{max}}}{F_{spont} - F_{\text{max}}} \right) \]

Where \( g_{\text{max}}(F) \) is given by:

\[ g_{\text{max}}(F) = \frac{E_{\text{max}}}{2} [\cos(2\pi x) + 1] \]

Where \( E_{\text{max}} \) is defined by the minimum and maximum 8-bit speed range \( V_r = (150, 250) \) used for the robot control. \( E_{\text{max}} = 250 - 150 = 100. \)

Substituting for \( x \) in \( g_{\text{max}}(F) \) gives:

\[ g_{\text{max}}(F) = \frac{E_{\text{max}}}{2} [\cos(2\pi \phi) + 1] \]

where \( \phi = -\frac{1}{2} \left( \frac{F - F_{\text{max}}}{F_{spont} - F_{\text{max}}} \right) \)
**Derivation of** \( g_{\text{min}}(F) \)

Similar to the derivation of \( g_{\text{max}}(F) \), the required mapping is given by:

\[
(0, F_{\text{spont}}) \rightarrow (-E_{\text{min}}, 0) \tag{A.8}
\]

Therefore, domain conversion is given by:

\[-\frac{1}{2} \leq x \leq 0 \quad \rightarrow \quad 0 \leq F \leq F_{\text{spont}}\]

Which gives,

\[
x = -\frac{1}{2} \left( \frac{F}{F_{\text{max}}} \right)
\]

Where \( g_{\text{min}}(F) \) is given by:

\[
g_{\text{min}}(F) = -\frac{E_{\text{min}}}{2} \left[ \cos(2\pi x) + 1 \right]
\]

For errors calculated in the case \( F < F_{\text{spont}} \), the maximum error \( E_{\text{min}} \) is limited to 25% of its current speed \( V_r(t) \):

\[
E_{\text{min}} = \frac{1}{4} (V_r(t) - \hat{V}_r)
\]

where \( \hat{V}_r = 150 \) (the lowest 8-bit speed used)

\( g_{\text{min}}(F) \) is therefore defined as:
\[ g_{\text{min}}(F) = -\frac{E_{\text{min}}}{2} [\cos(2\pi \phi) + 1] \]

\[ g_{\text{min}}(F) = -\frac{1}{2} [\cos(2\pi \phi) + 1] \cdot \frac{1}{4} [V_r(t) - \dot{V}_r] \]

where \( \phi = -\frac{1}{2} \left( \frac{F}{F_{\text{max}}} \right) \)
B. Publications and Conference Proceedings

Some of the work presented in this thesis has been published and presented at scientific conferences:

Chapter 2

Peer-reviewed publications


Conference proceedings

Chapter 3

Peer-reviewed proceedings


Conference proceedings


Chapter 4

Peer-reviewed proceedings


Conference proceedings

- Peterson K, Ejaz N, Krapp HG. 9th Gottingen Meeting of the German Neuroscience Society (2011)

Chapter 5

Peer-review publications

- Ejaz N, Tanaka RJ, Krapp HG. Neural response properties of the Blowfly H1 in closed-loop. Frontiers in Neural Circuits (In prep, abstract selected for special call)
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