

CORRECTION

Correction: Flight control of fruit flies: dynamic response to optic flow and headwind (doi:10.1242/jeb.153056)

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There was an error published in *J. Exp. Biol.* (2017) **220**, 2005–2016 (doi:10.1242/jeb.153056).

In Materials and Methods, ‘Virtual reality flight platform’, the units for pitch torque were incorrect. The corrected sentence is given below.

Although this configuration cannot separate the thrust force and pitch torque generated by the flies, it was assumed that the pitch torque produced [estimated to be $3\times$ greater than that of *Drosophila melanogaster* ($\sim 10^{-2}$ N μ m; Sugiura and Dickinson, 2009), or $\sim 3\times 10^{-2}$ N μ m, which translates to a force of ~ 3 μ N projected onto the transducer] is significantly lower than the mechanically amplified thrust (40–160 μ N projected onto the transducer, peak-to-peak).

We apologise to the authors and readers for any inconvenience this may have caused.

RESEARCH ARTICLE

Flight control of fruit flies: dynamic response to optic flow and headwind

Kiaran K. K. Lawson^{1,*} and Mandyam V. Srinivasan^{1,2,*}

ABSTRACT

Insects are magnificent fliers that are capable of performing many complex tasks such as speed regulation, smooth landings and collision avoidance, even though their computational abilities are limited by their small brain. To investigate how flying insects respond to changes in wind speed and surrounding optic flow, the open-loop sensorimotor response of female Queensland fruit flies (*Bactrocera tryoni*) was examined. A total of 136 flies were exposed to stimuli comprising sinusoidally varying optic flow and air flow (simulating forward movement) under tethered conditions in a virtual reality arena. Two responses were measured: the thrust and the abdomen pitch. The dynamics of the responses to optic flow and air flow were measured at various frequencies, and modelled as a multicompartment linear system, which accurately captured the behavioural responses of the fruit flies. The results indicate that these two behavioural responses are concurrently sensitive to changes of optic flow as well as wind. The abdomen pitch showed a streamlining response, where the abdomen was raised higher as the magnitude of either stimulus was increased. The thrust, in contrast, exhibited a counter-phase response where maximum thrust occurred when the optic flow or wind flow was at a minimum, indicating that the flies were attempting to maintain an ideal flight speed. When the changes in the wind and optic flow were in phase (i.e. did not contradict each other), the net responses (thrust and abdomen pitch) were well approximated by an equally weighted sum of the responses to the individual stimuli. However, when the optic flow and wind stimuli were presented in counterphase, the flies seemed to respond to only one stimulus or the other, demonstrating a form of 'selective attention'.

KEY WORDS: Flight control, Flight thrust, Fruit fly, Insect, Optic flow, System identification

INTRODUCTION

Insects in flight can be portrayed as a black-box multisensory control system: continuous information, such as vision, air flow and scent, is gathered from the sensory organs, then combined and processed in the brain to generate appropriate behavioural responses (Taylor, 2001). Despite their minute brain and limited processing capabilities, insects are able to effectively utilise the sensory information that is available to them – where vision and air speed sensing are most crucial in flight (Taylor and Krapp, 2007) – to

perform a range of complex tasks. Some examples are obstacle avoidance (Muijres et al., 2014; Serres et al., 2008; Srinivasan et al., 1999), regulation of flight speed (Baird et al., 2005; Portelli et al., 2011; Srinivasan et al., 1996), regulation of flight altitude (Portelli et al., 2010) and orchestration of smooth landings (Baird et al., 2013; Srinivasan et al., 2000; van Breugel and Dickinson, 2012). All of these refined behaviours are generated through three main actuators of the insect body – the wings, abdomen and legs – which, in combination, produce the forces and torques required to control their flight in six degrees of freedom (Fry et al., 2005; Zanker, 1988).

In order to reveal and understand how these small flying creatures process and dynamically control flight efficiently in complex environments, many approaches have been taken with various perspectives over the last few decades. The most significant physical component of insect flight is their wing-flapping locomotion, which is responsible for the generation of effective lift (i.e. the net upward force counteracting the insect's weight), thrust [the forward force perpendicular to the effective lift (Osborne, 1951)], and the control of yaw and roll (Heisenberg and Wolf, 1979). Many species of flies, which only have two wings, can only flap their wings in a fixed pattern, and therefore produce a flight force that is oriented along a single, fixed direction relative to their body axis (24 deg for *Drosophila*, and 29 deg for *Musca*) (Dickinson and Muijres, 2016; Götz and Wandel, 1984; Muijres et al., 2014). Because of this constraint, the forces that are generated along and perpendicular to the body axis are always proportional to each other, regardless of the flight conditions. Thus, the ratio of effective lift to thrust can be redirected only by adjusting the pitch of the body.

In conjunction with their wing flapping locomotion, flying insects constantly adjust their abdomen pitch (Luu et al., 2011; Taylor et al., 2013) and move their legs frequently during flight (Dudley, 2000). Leg movement during flight occurs when the air flow is turbulent, in order to prevent roll motion of the insect, as stretching the legs increases the moment of inertia (Combes and Dudley, 2009), allowing improved steering performance (Zanker, 1988). Pitch angle adjustments during flight, however, seem to have a number of functions. Early research conducted by David (1978) suggested that the body angle of *Drosophila hydei* is inversely related to the flight speed. On this basis, Luu et al., (2011) proposed that the pitch angle adjustments are a 'streamlining' response, where insects actively try to minimise the effect of drag force when flying at high speeds to decrease the thrust required to maintain their current speed, increasing the efficiency of flight. This effect was experimentally shown in that study using tethered honeybees, which were exposed to a constant forward motion visual stimulus inside a virtual reality arena. Building on this work, Taylor et al. (2013) investigated and modelled the steady-state streamlining response of honeybees when exposed to a combined input composed of steady optic flow and airflow during tethered flight in a virtual

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environment. By measuring the abdomen pitch angle when honeybees were exposed to various combinations of steady optic flow and airflow, Taylor et al. (2013) developed a nonlinear model describing the open-loop steady-state pitch angle response of tethered honeybees, which involved summation and multiplication of the two sensory inputs, thresholded by a sigmoid function.

The experiments conducted by Taylor et al. (2013) provided a good initial characterisation of the steady-state response of honeybees exposed to steady wind and optic flow stimuli in open-loop virtual environments, but did not explore the dynamic responses of thrust or abdomen pitch when the stimuli change with time. Nor did that study investigate other possible reasons for the changes in abdomen pitch that many flying insects display. Furthermore, Dyhr et al. (2013) proposed and confirmed, for hawkmoths (*Manduca sexta*), that pitch reorientation rotates the thorax, resulting in redirection of the flight force, and assists in flight stabilisation. Also, by measuring the pitch response to a vertically oscillating visual stimulus under open-loop conditions, they found that the pitch control system can be adequately modelled as a first-order high-pass filter, with an additional pure time delay of 41 ms. Tanaka and Kawachi (2006) conducted similar tethered flight experiments on bumblebees (*Bombus terrestris*), where a visual grating (generated by a panoramic matrix of LEDs surrounding the insect) was oscillated vertically in a sinusoidal manner. The bumblebees' effective lift force was measured for four different stimulus oscillation frequencies, and the response was treated as an open-loop control system in order to model the bees' intrinsic flight controller. From these results, the open-loop flight response of the bumblebees was fitted to a second-order low-pass filter transfer function model – where the transfer function structure was adopted from studies of optimal human pilot responses (McRuer and Graham, 1964) – and compared against the actual bumblebee response. Contrary to the hawkmoth's pitch response, the bumblebee's lift transfer function was in the form of a low-pass filter, and the response was surprisingly faster in comparison to the pilot-vehicle system, and was in phase for all tested frequencies. The bee's response also exhibited a greater response gain than humans at lower frequencies, confirming the superiority of its flight controller despite its limited processing capabilities.

In this study, we investigate the open-loop response of female Queensland fruit flies [*Bactrocera tryoni* (Froggatt 1897)] in tethered flight inside a virtual reality arena. Although this particular species has not been previously investigated in the context of flight behaviour, it was chosen as the experimental subject for three reasons. Firstly, unlike many other fly species, this species is physically capable of varying its abdomen pitch over a wide range of angles, as the joint between the thorax and abdomen is thin. Secondly, the body length (6–8 mm) is approximately two to three times longer than that of *Drosophila melanogaster*, and yet the wingbeat frequency is similar to that of *Drosophila* and the honeybee. Finally, the wingspan (10–12 mm) is also approximately double that of *Drosophila*, but half that of honeybees. These above reasons place Queensland fruit flies midway between these two commonly studied species.

Many studies, including ones discussed earlier, have measured the effective lift response of insects exposed to visual stimuli that provide vertical motion in the frontal or lateral visual fields (e.g. Dickinson et al., 1998; Gaetz et al., 2010; Straw et al., 2010). In this study, we measure the thrust of the flies exposed to a horizontally oscillating stimulus, as horizontal motion is more dominant and natural for flying insects. As most flies cannot produce a negative thrust relative to their longitudinal axis (and

therefore cannot fly backwards) (Götz and Wandel, 1984), a constant forward motion was added to the horizontal oscillation to make the optic flow non-negative at all times. It was assumed that this would generate a natural baseline response, and not affect the dynamic response of the flies. In addition to the optic flow stimulus, a laminar headwind stimulus of oscillating magnitude was also used to extend the findings of Taylor et al. (2013), and study the dynamic responses to these stimuli. The abdomen pitch angle of the flies was also analysed to investigate the change in magnitude and reaction speed of the pitch angle to the dynamic variations of the two stimuli.

Although it is now well established that flying insects rely heavily on visual stimuli in order to navigate through cluttered and highly dynamic environments (Floreano and Zufferey, 2010; Srinivasan, 2011), their dependence on other sensory organs and the mechanisms used to integrate multisensory information in their flight regulator are not yet well understood. This study endeavours to model a multi-input multi-output (MIMO) linear control system of flying fruit flies, in order to further these understandings.

MATERIALS AND METHODS

Fly preparation

Experiments were conducted using female Queensland fruit flies (*Bactrocera tryoni*) varying in age between 2 weeks and 2 months, supplied from the Department of Agriculture and Fisheries, Queensland Government. The flies were housed in a cage maintained at room temperature (24°C) and were fed sugar and water. Flies were selected randomly for experimentation, then cold anaesthetised by placing the flies (concealed in a 50 ml plastic tube) inside a standard freezer (−15±5°C) for 1–2 min, and finally tethered to a vertical metal rod (~16 mm long, bent at the bottom to provide a ~3 mm horizontal section for fly attachment) while still anaesthetised. The attachment was performed by applying a dental cement solution, cured in near-UV light (shade modification kit, SDI, Bayswater, VIC, Australia), to the thorax (near the centre of mass), between the wings. Between experiments, the flies were placed tethered inside a humid, temperature-regulated box at 30±3°C. The internal temperature of the virtual reality platform was also maintained at the same temperature level throughout the duration of the flight experiments, in order to maximise behavioural activity.

Virtual reality flight platform

Tethered flies were supplied with small amounts of an aqueous glucose solution, and then rested for 20–30 min before a flight experiment was conducted, in order to adjust to the new environment. Flies ready for experimentation were attached to a metal mount located in the centre of the arena, which connected mechanically to the tip of a force transducer (403A, Aurora Scientific, Aurora, ON, Canada). The force transducer was held by an articulated arm (MA61003, Noga, Shlomi, Israel), which was placed on a vibration isolation system (66 Series TableTop CSP, TMC, Peabody, MA, USA; www.techmfg.com) to avoid environmental vibrations. The transducer was calibrated by placing a range of known weights directly onto the probe of the transducer when it was oriented vertically. A mechanical pivot, as shown in Fig. 1C, was used to transmit the force generated by the fly to the transducer probe. This arrangement mechanically amplified the thrust generated by the fly by a factor of 2.12. Although this configuration cannot separate the thrust force and pitch torque generated by the flies, it was assumed that the pitch torque produced [estimated to be 3× greater than that of *Drosophila melanogaster* (~10^{−2} N mm; Sugiura and Dickinson, 2009), or ~3×10^{−2} N mm, which translates to a force of ~3 mN projected on to the transducer]

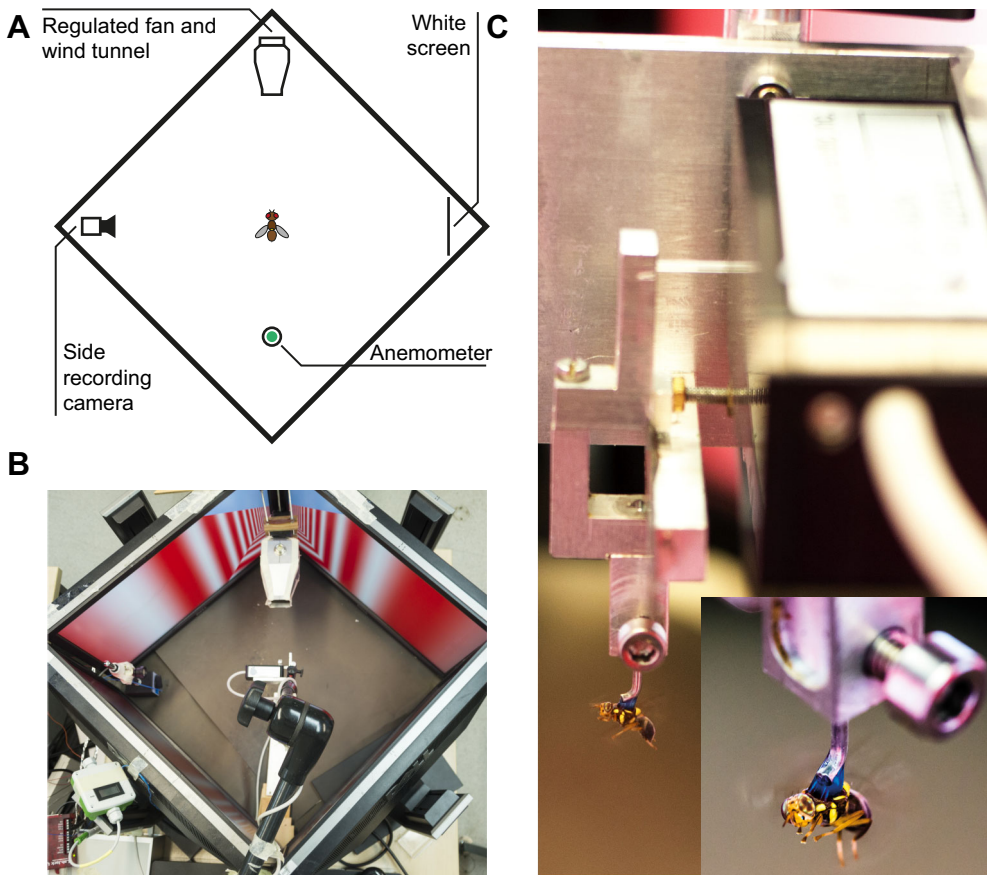


Fig. 1. The virtual reality flight arena. (A) Schematic top view of the flight arena (objects not to scale). (B) Photo of the top view of the flight arena. (C) Side view of the flight arena, as observed from the camera position, with a tethered fly attached to the force transducer. An enlarged side-frontal view of the fly is overlaid in the lower right corner.

is significantly lower than the mechanically amplified thrust (40–160 μN projected onto the transducer, peak-to-peak). The force transducer recorded the thrust at a rate of 1 kHz, while the camera (Firefly, FLIR, BC, Canada) located on the side was used to record and analyse the abdomen pitch of the flies in real-time at a rate of 30 Hz. As the raw thrust measurements contained high-frequency components generated from wingbeats in addition to the slowly varying net thrust output in response to the stimuli (which was the response of interest), the wingbeat frequency components were filtered out using a low-latency, 154th-order finite impulse response (FIR) filter (at 1 kHz sampling rate) with a cut-off frequency of 10 Hz.

A small white screen was placed on the corner of the arena opposite to the camera, in order to obtain a high-contrast silhouette of the fly, for accurate measurement of the pitch. The measurement and analysis of the pitch from the camera images was performed using a custom-written program in C++, as described in Taylor et al. (2013). Inside the arena, flies were exposed to optic flow presented by four surrounding monitors (Dell 2209WA, 1680×1050 resolution, 60 Hz refresh rate) and also to headwind, generated by two pulse width modulation (PWM)-controlled fans (TurboFan 12VDC, 40×28 mm, 20,000 rpm, NMB Technologies Corp., Novi, MI, USA) positioned in front of the fly. The fans were placed in a square-shaped wind tunnel to minimise the turbulence of the flow. The fan assembly caused only a minor occlusion of the visual stimulus in front of the fly's visual field, measured to be 8 deg horizontally and 9 deg vertically. An anemometer (EE-65VB, E+E Elektronik GmbH, Engerwitzdorf, Austria) was also placed behind the fly, to measure and calibrate the speed of the wind stimulus. Analogue data acquisition (of the thrust and wind), as well as the control of optic flow and headwind speeds, were executed by a desktop computer

[Intel i7-920 CPU (four cores @ 2.67 GHz), 2.5 GB RAM, Windows XP SP 3] with two NVIDIA GeForce GTX 260 video cards and a USB DAQ device (LabJack U3-HV, Lakewood, CO, USA). Customised software, modified from that created by Luu et al. (2011) (available upon request), was used to generate the visual environment through the monitors, and to control the headwind. The four monitors were arranged in a diamond-shaped formation to provide a near-panoramic visual environment for the insect – note that the monitors' bezels prevent a full 360 deg azimuthal visual field, thus resulting in 3 deg gaps at each corner of the monitor setup. The visual stimulus provided by the monitors mimicked the effect of forward flight along an infinitely long tunnel (as a 3D virtual environment), with red and white sinusoidal gratings (with a spatial frequency of 0.014 cycles deg^{-1}) on the two side walls. The optic flow generated by the moving gratings is specified in terms of the angular velocity (in deg s^{-1}) experienced by the fly's visual system in its lateral visual field, in a viewing direction oriented at 90 deg to the fly's long axis, which corresponds to the direction that experiences the maximum angular velocity. The ground was set to be a simple black shade without texture, while the sky was set to a light-blue colour.

Linearity of fly responses

To confirm that the control of flight can be modelled as a dynamic linear system for the species under test, an experiment was conducted in which the flies were exposed to stimuli of gradually increasing oscillatory amplitude. Three conditions were tested, where either optic flow or wind was oscillated, and also where both stimuli were oscillated in phase. The optic flow stimulus commenced oscillation with a peak amplitude of 25 deg s^{-1} and increased gradually with time to a final amplitude of 200 deg s^{-1} ,

around a baseline speed of 200 deg s^{-1} . For the headwind, the peak amplitude increased gradually with time from a minimum of 0.05 m s^{-1} to a maximum of 0.5 m s^{-1} , around a baseline wind speed of 1.0 m s^{-1} . Both stimuli were oscillated at $1/8 \text{ Hz}$, and the amplitudes were increased linearly over the duration of the experiment, which was set as 210 s . The recorded responses of abdomen pitch and net thrust were then fitted to sinusoidal functions with linearly increasing amplitude, in order to assess the linearity of the response (results shown in Fig. 2).

Virtual flight experiments

In each experiment, the visual and wind stimuli were presented to tethered fruit flies for approximately 3 min . The optic flow and wind speeds were oscillated in a cosinusoidal manner (i.e. the stimulus speeds were set to the maximum initially) to investigate the flies' response to a dynamically changing environment. Optic flow was presented in the progressive front to back direction and its magnitude was oscillated between 50 and 450 deg s^{-1} , while the headwind (at the position of the fly) was oscillated between 0.5 and 1.5 m s^{-1} . These values were chosen based on a study of thrust and abdomen pitch responses in honeybees (Taylor et al., 2013). (We note, however, that their study did not vary the stimuli dynamically.) The visual and wind stimuli were oscillated between the amplitudes stated above at the following frequencies: $1/32$, $1/16$, $1/8$ and $1/4 \text{ Hz}$. The upper frequency was limited to $1/4 \text{ Hz}$, as the wind speed could not be modulated accurately at higher frequencies because of the unavoidable latencies in using a fan to deliver accurate, time-modulated airflow. For each tested frequency, four different conditions were examined: (1) only optic flow (OF) was modulated while the wind speed (WS) was constant at 1.5 m s^{-1} (vOFcWS – where 'v' signifies 'varying' and 'c' signifies 'constant'); (2) only wind speed was modulated while the optic flow was constant at 450 deg s^{-1} (cOFvWS); (3) optic flow and wind speed were both oscillated in phase (vOFvWS); and (4) optic flow and headwind were both oscillated, but the headwind was in anti-phase with optic flow (cPhase).

For experiments where only one stimulus was oscillated, the constant magnitude of the other (steady) stimulus was set to the maximum value in the experimental range instead of the mean, as

preliminary tests indicated that using the mean value (i.e. $\text{OF}=250 \text{ deg s}^{-1}$, $\text{WS}=1.0 \text{ m s}^{-1}$) did not invoke sufficient activity from the flies. $N=20\text{--}22$ fully responsive flights (disregarding tests where the fly did not fly for the entire experimental duration) were conducted for each combination of experimental condition and stimulus oscillation frequency. The stimulus exposure time for each experiment was set to 150 s for the high frequency tests ($1/4$ and $1/8 \text{ Hz}$) and 180 s for the low frequency tests ($1/16$ and $1/32 \text{ Hz}$), exposing the flies to at least 37, 18, 11 and 5 full stimulus oscillation cycles, respectively. On average, four virtual flight experiments were conducted per fly, as further experiments caused a reduction in responsiveness.

RESULTS

Linearity of responses

The thrust and abdomen pitch responses to the ramped sinusoidal inputs (as described in the Materials and methods) are shown in Fig. 2. From this figure, and from the analysis of the response in the Appendix (Fig. A1), it is evident that both the abdomen pitch and the thrust react approximately linearly to changes in oscillatory amplitude of the optic flow and headwind. Although there were some response periods with over- and undershooting amplitudes in comparison to the fit, the general trend of the responses followed the linearly increasing sinusoidal amplitude model, supporting our assumption that the various components that underlie the flight control system under study can adequately be modelled as linear systems.

Abdomen pitch and thrust responses to sinusoidal modulation of optic flow and wind

Of the 545 flight experiments conducted from a total of 136 flies, 331 (60.7%) tests were successful, where the fly responded to the stimulus for the entire duration of the flight. This success rate in tethered flight did not depend upon the oscillation frequency or other properties of the stimulus. Among the unsuccessful flight tests (which were not included in the analysis), there were a few different types of responses. Some flies completely ignored the stimulus and only moved their legs randomly, without any wing-flapping motion. Another group showed an abdomen pitch response to the stimulus

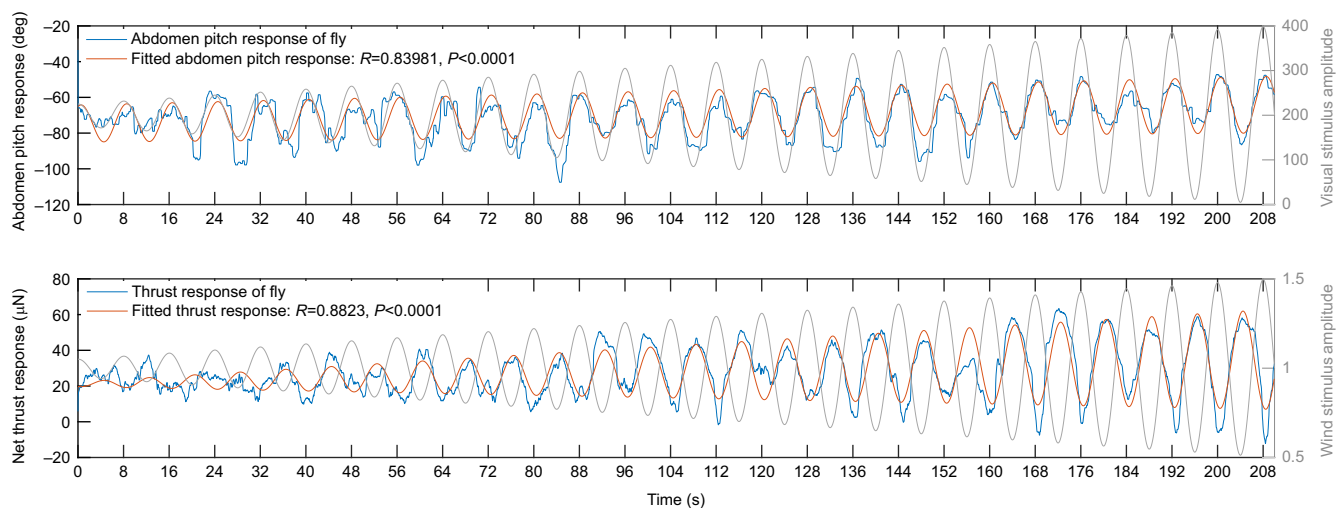


Fig. 2. Dynamic changes in response amplitude of abdomen pitch and net thrust recorded from one fly placed in an oscillatory virtual arena with linearly increasing oscillation amplitudes of both visual and wind stimuli (at a frequency of 0.125 Hz) over the course of the experiment. In this particular case, both optic flow and headwind were modulated with steadily increasing amplitudes. The red curves show the fits of a ramped sinusoid to the response, as described in the Appendix.

without any wing-flapping movement (although some flies tended to ‘glide’ with their wings stretched out when stimuli had high amplitudes), while a third group of flies flew intermittently during the experiment. In the successful flight tests, however, a vast majority of the flies exhibited similar responses, with small variations in abdomen pitch angle amplitude. Yet, a small group of these flies exhibited a peculiar response where they would display an active response in one output (thrust or pitch) while the other output remained completely static. These responses were excluded from further analysis. The variety of responses observed may have been due to the relatively wide range in the age of flies tested, or the slight variations in the amount and location of dental cement applied to tether the flies, as well as the exact orientation in which they were tethered.

For each experiment, approximately 20 s of data was recorded before and after exposure to the stimulus to ensure that the entire response profile was captured (including control baseline experiments in which there was no stimulus). The majority of flies required exposure to visual and wind stimuli to initiate and maintain active flight. However, some flies began flight naturally immediately after they were placed inside the virtual reality arena, and continued to fly even after the stimulus was terminated, as shown for the pitch response in Fig. 3. In the responses shown in Fig. 3, as well as in the majority of responses observed under all experimental conditions except for the counter-phase (cPhase) experiments, the abdomen was raised when the magnitude of the input stimulus (optic flow or wind speed) was high, and lowered when the magnitude was low. The amplitude of the oscillation of the abdomen pitch varied in phase with the magnitude of the oscillation of the input stimulus. In contrast, the thrust response varied in a counter-phase manner, attaining its maximum value moments after either stimulus reached its lowest speed. In other words, the thrust response was at a maximum when the optic flow or the air flow was at its lowest magnitude. Flies that continued to fly in the absence of any stimulus exhibited a large thrust response, and the abdomen was completely lowered.

In order to quantify and summarise the response obtained from each experiment, successive periods of the pitch and thrust responses were superimposed and averaged, as shown in Fig. 4. The amplitude, phase and mean offset of the response were computed by fitting a sinusoidal function to the average response with the frequency set to the modulation frequency. This sinusoidal fit eliminated the bulk of the noise in the data, and summarised the results of each experiment in terms of three response parameters: the amplitude, phase and mean value. This procedure was also advantageous when modelling the fly’s control system, as the inputs and outputs could be treated as sinusoids with the same frequency. In the cPhase experiments, the phase of the optic flow was used as the 0 deg phase lag reference; therefore, the wind stimulus was, by definition, 180 deg out of phase.

Although fitting the responses to sinusoids is an efficient way of summarising the results of each experiment, this procedure relies on the assumption that the flies’ pitch and thrust responses resemble sinusoids with the same frequency as the input. This would only be true if the dynamical system is perfectly linear. The majority of the responses were indeed close to sinusoidal, as revealed by fitting a sinusoidal waveform to the mean response curve: 66.5% of the pitch responses and 76.4% of the thrust responses had R^2 values greater than 0.7, while 8.2% of both pitch and thrust responses had R^2 values less than 0.3. Thus, the responses that did not fit a sinusoidal waveform were a minority and had little effect on the overall average response. Furthermore, the fitted phase lag values became highly unreliable as the response amplitude approached 0, because the response was then buried in the noise and its peak could not be located reliably along the noisy, near-horizontal line. The responses with low amplitude were detected and refitted 20 times (with randomly varying initial guesses), and the fit with the largest R^2 value was taken to provide the most reliable measurement of the phase of the response.

The curve-fitting method was applied individually to each experimental trial, and then further summarised for each test condition by finding the mean values of each parameter. Fig. 5

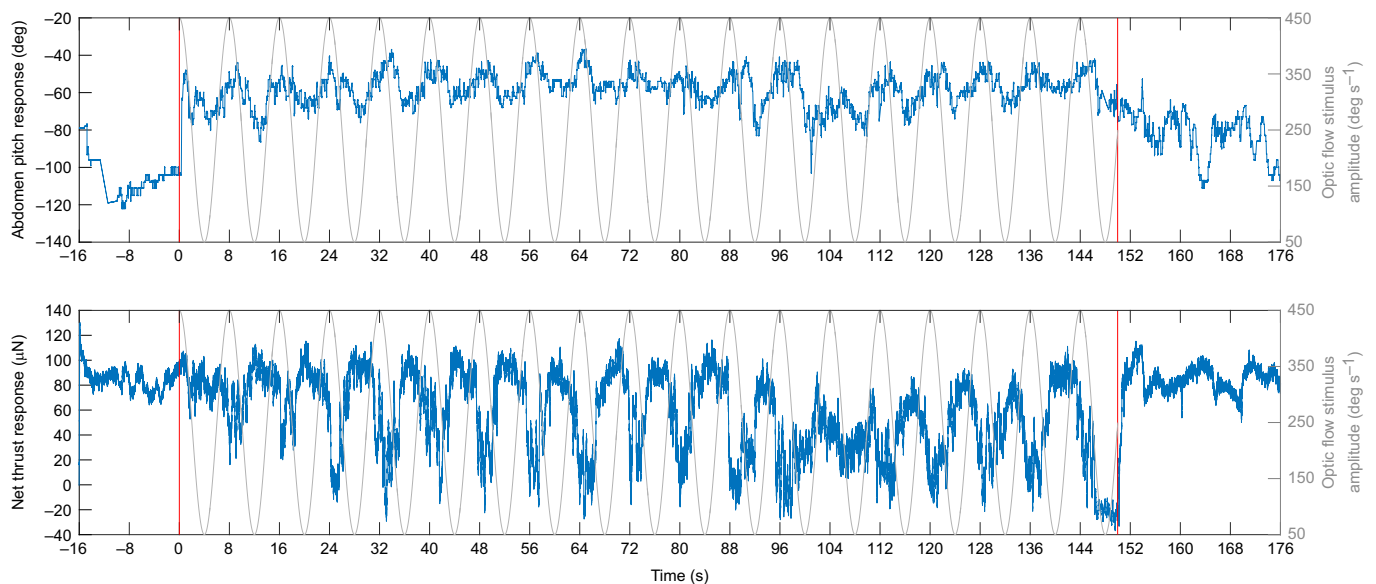


Fig. 3. Example of the time course of the pitch (top) and thrust (bottom) response recorded in a single experiment. In this experiment, only the optic flow was modulated at a rate of 1/8 Hz. As indicated by the red lines, the stimulus exposure begins at $t=0$ s and terminates at $t=150$ s. The grey cosine curve shows the magnitude of the stimulus. For pitch angles, higher values signify a streamlining response (i.e. the abdomen is more aligned with the thorax), and lower angles represent a lowered abdomen.

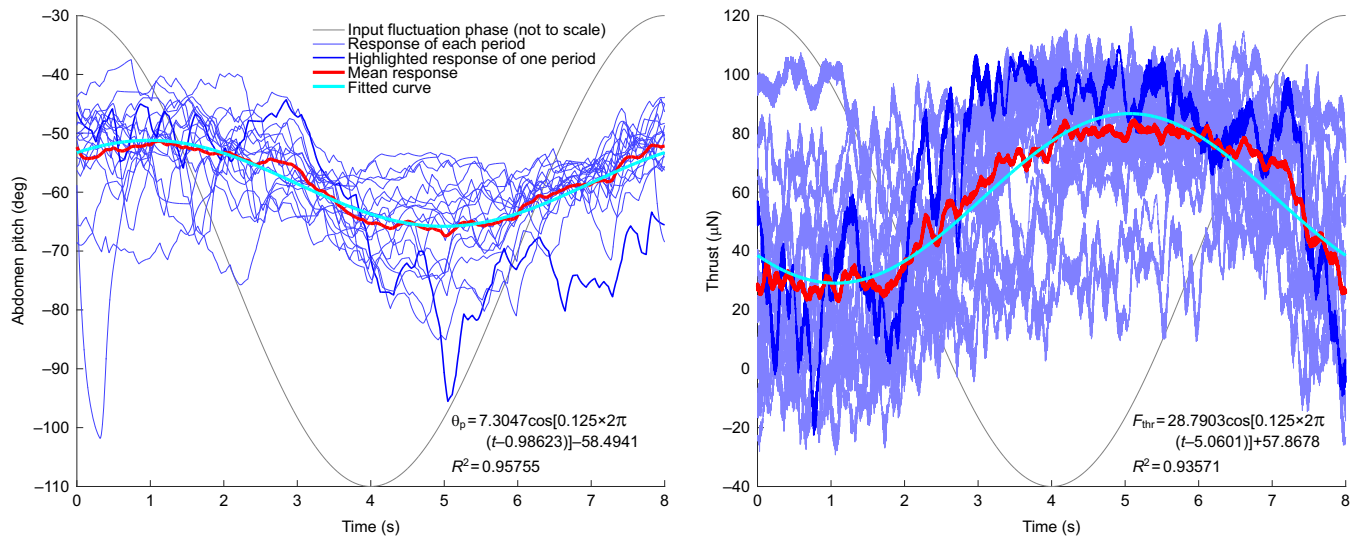


Fig. 4. The summarised responses of pitch and thrust obtained from a single experiment (same measurement as Fig. 3). Light blue lines show individual responses from each period of the stimulus cycle; one randomly selected response is highlighted by a darker blue line. The red line indicates the mean response calculated from all responses. The cyan curve shows a cosine fit to the average response with parameters indicated on the bottom right of the plots. Grey curves indicate the shape and timing of the input optic flow stimulus (not to scale). θ_p and F_{thr} show the equations of the fitted cosine curve for the abdomen pitch and net thrust, respectively.

shows the overall mean responses of both abdomen pitch and thrust for each test condition for all of the four tested frequencies, while Fig. 6 shows the frequency response relationships as bar charts, analogous to Bode plots. The mean offset values of the responses are ignored here, as the main interest is the change in response caused by changes in stimulus magnitude.

The abdomen pitch response of the flies displayed characteristics similar to those of a low-pass filter, where the amplitude decreased

almost linearly, and the phase lag increased at a growing rate, as the frequency increased exponentially. Over all tested frequencies, the abdomen pitch response was fastest (with the smallest phase lag) when both stimuli were varied concurrently in phase; varying only optic flow was marginally faster than varying only headwind, and the abdomen pitch response was slowest when the stimuli were oscillated in a counter-phase manner. In terms of amplitude, the largest amplitudes of the pitch and thrust response were obtained when both stimuli were in

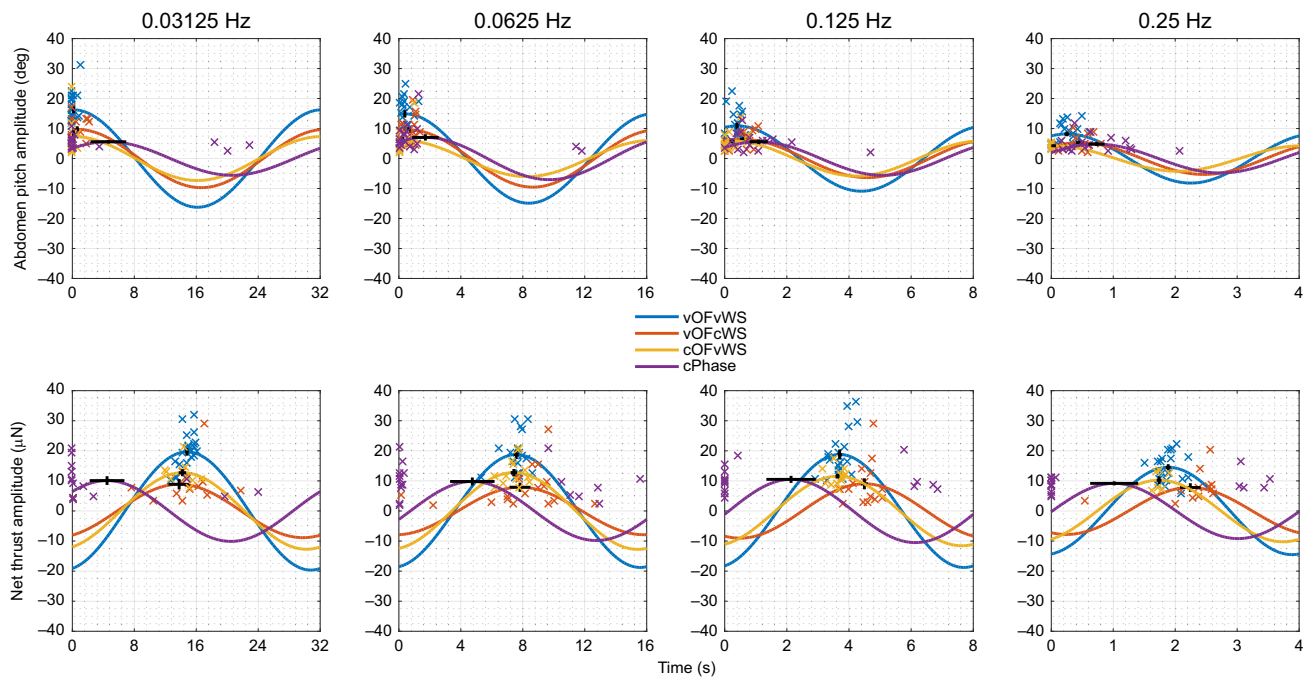


Fig. 5. Summary of all pitch and net thrust responses obtained over different frequencies. The upper row shows the pitch responses, while the bottom row shows the thrust responses. Each column shows the responses to a specific stimulus oscillation frequency. Each scatter point represents the peak amplitude and phase lag obtained from one experiment, while the sine curve shows the average response, obtained by fitting the responses of all flies tested under the same condition (with the baseline offsets ignored). Sample sizes in order of increasing stimulus frequency: vOFvWS: $n=22, 19, 21, 20$; vOFcWS: $n=14, 18, 15, 12$; cOFvWS: $n=10, 13, 13, 6$; cPhase: $n=14, 18, 15, 16$ (v, varying; c, constant; OF, optic flow; WS, wind speed; cPhase, counter phase). Error bars of the averaged fitted responses indicate ± 1 s.e.m.

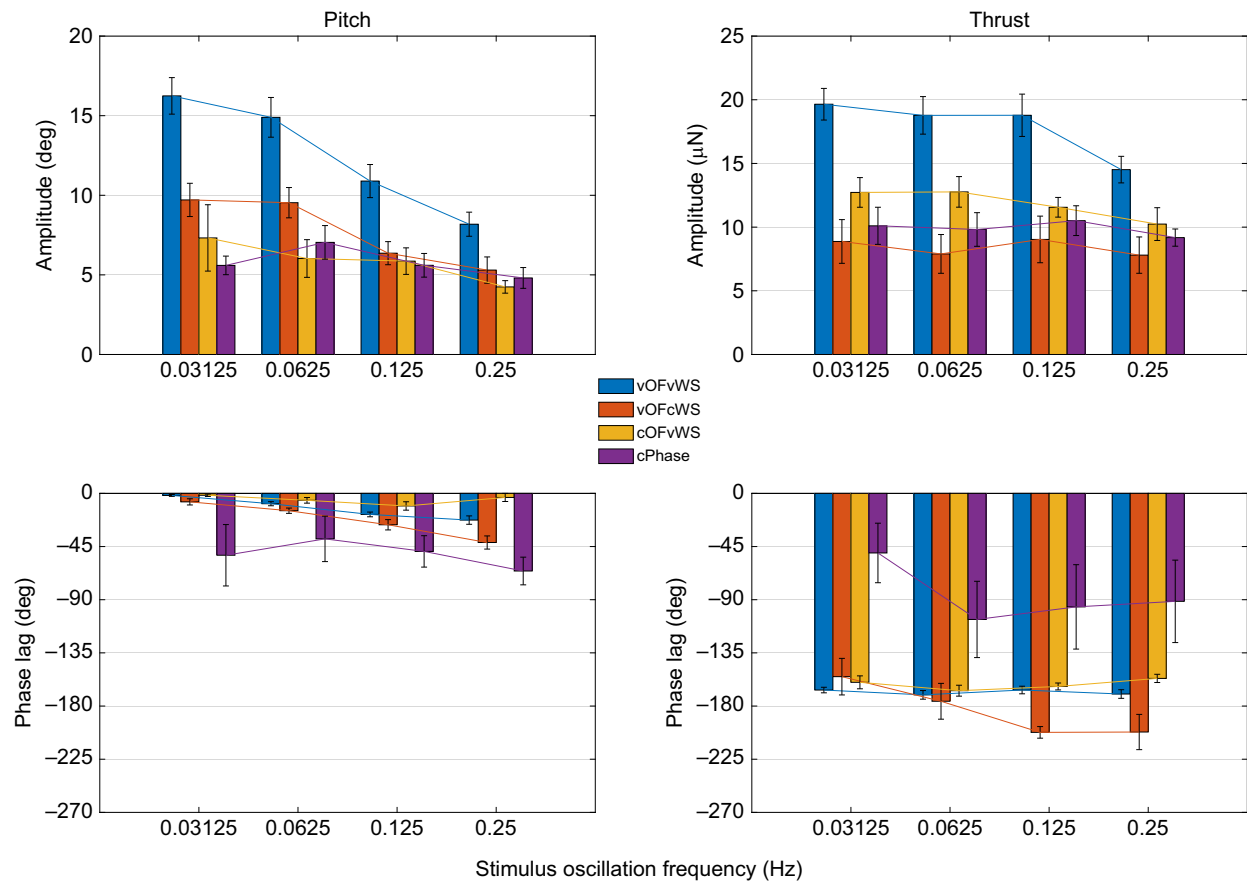


Fig. 6. Amplitude and phase response of the fruit flies for pitch and net thrust. The left and right panels show the pitch and thrust responses, respectively. The upper panels show the frequency dependence of the response amplitude under different experimental conditions, while the lower panels show the frequency dependence of the phase shift. Error bars indicate ± 1 s.e.m.

phase. Smaller response amplitudes were observed when only one of the stimuli was modulated. The cOFvWS and cPhase experiments generated responses of the lowest (and similar) amplitude.

The characteristics of the thrust response were different in comparison to the abdomen pitch response. Unlike the pitch response, the magnitude of the thrust response remained nearly constant across the different frequencies, except for a slight attenuation at 0.25 Hz. Again, unlike the pitch responses, which tended to remain in-phase with the input stimuli, the thrust responses were approximately 180 deg out of phase even at the lowest frequency tested, except for the counterphase experiments (as discussed further in the Discussion). The phase lags of the thrust for the three stimulus conditions (excluding cPhase) were highly correlated, except where the vOFcWS experiments showed a greater increase in lag with frequency, compared with the other tested conditions. The largest thrust response was observed in vOFvWS experiments, as with the abdomen pitch response; however, the thrust response was larger for the cOFvWS stimulus when compared with the vOFcWS stimulus response. The smallest response was observed in the vOFcWS experiments, contrary to the relationship seen in the abdomen pitch response.

Thus, for each of the tested stimulus conditions, the flies displayed different control system characteristics. In summary, the results indicate that the amplitudes of the pitch and thrust responses are largest when the optic flow and wind stimuli are modulated in phase, and are significantly lower when only one of the stimuli is modulated. However, the cOFvWS and vOFcWS experiments

display different characteristics, where modulating only the wind produces a larger and faster thrust response, and modulating only the optic flow produces a stronger pitch response.

Inspection of the responses of individual flies to the cPhase experiments in Fig. 5 reveals a bimodal response in both pitch and thrust. The abdomen pitch response (also shown in Fig. 5) indicates that, in the cPhase experiment, the majority of flies followed only the optic flow, while there were a few that seemed to be responsive only to the wind stimulus, although the variance in phase was high between samples. The thrust responses, in contrast, were divided almost equally into two categories, where one half of the flies reacted solely to the wind, and the other half reacted only to the optic flow, judging from the bimodal nature of the response phases.

Dynamic models of the responses

We modelled the dynamics of the pitch and thrust responses, assuming that (1) each of these responses behaves linearly with respect to each of the inputs, and (2) the interactions between the two responses are linear.

Using these two assumptions, the input–output characteristics of each of the four input–output combinations was modelled by transfer functions taking the form of a second-order filter in the complex frequency (s) domain with a constant time delay of τ seconds, described by:

$$G(s) = K \frac{1 + as}{(1 + bs)(1 + cs)} e^{-\tau s}. \quad (1)$$

The coefficients (K is the gain, a is the zero constant, b and c are pole constants, and τ is the constant time delay) were determined using the System Identification Toolbox of MATLAB, which utilised the Gauss–Newton iterative method of optimisation. A system with two poles and one zero was found to be sufficient to model each component of the flies’ flight controller. As in classic mechanics, motions can be adequately described using derivatives of up to second order – higher-order derivatives of motion are negligible. Furthermore, a study modelling the effective lift response of bumblebees (Tanaka and Kawachi, 2006) determined that second-order models were adequate and the most appropriate.

Once these parameters of the transfer function were determined (as shown in Table 1), the resulting theoretical gains and phases of the abdomen pitch and thrust responses were obtained by feeding the theoretical inputs to the corresponding transfer function. The summation of the complex responses (gain and phase) at various frequencies, as predicted by the transfer functions, is illustrated in the block diagram (Fig. 7A). Finally, the output of the model was compared with the experimental results to assess the accuracy of the fit, as illustrated in Fig. 7B.

DISCUSSION

Our results suggest that fruit flies dynamically modulate their abdomen pitch and thrust when exposed to visual and wind stimuli that are constantly varied. Both the pitch and thrust responses were largest when the two stimuli were modulated in phase. When the stimuli were modulated in opposing phase, each fly seemed to prefer one stimulus over the other.

The abdomen pitch response shown in Fig. 3 is not surprising, as it has been shown that flying insects demonstrate a streamlining response that increases progressively with optic flow or with air flow, although that study did not examine the dynamic characteristics of these responses (Taylor et al., 2013). However, the nature of the thrust response that we have observed is unexpected, as a previous study on bumblebees (Tanaka and Kawachi, 2006) suggested that the phase delay of the thrust response is significantly smaller than the value of 180 deg measured in our study. Thus, our experiments indicate that the thrust is highest when the optic flow or the air flow is at a minimum, and is lowest when either of these stimuli is at a maximum. This finding supports the notion that the observed thrust response is a mechanism for regulating flight speed by maintaining a constant magnitude of optic flow (Baird et al., 2005; Portelli et al., 2011; Srinivasan et al., 1996). Furthermore, this behaviour coincides with the flight behaviour observed in locusts, which produce a lower flight force and therefore decrease their altitude in strong headwinds (Kennedy, 1951), effectively holding the magnitude of the optic flow generated by the ground constant. This could be viewed as a means of conserving energy and maximising travel distance (Franceschini et al.,

2009). Our experiments indicate that the phase lag of the thrust response increases with higher stimulus oscillation frequencies, suggesting that the preferred phase delay of the thrust response is indeed 180 deg.

Our fitted model predicts a pure sensorimotor delay (latency) of the order of 0.025–0.05 s, which is consistent with many flying insect species; it was shown by Land and Collett (1974) that houseflies have a reaction time of approximately 30 ms, which was confirmed by a first order lead-lag model by Strydom et al. (2015). We assume that these numbers reflect response latencies that arise as a result of neuronal and motor delays, which are independent of stimulus frequency. The constant time delay of 48–49 ms observed in the flies’ optic-flow-driven abdomen pitch responses may reflect the time delay in the visual pathway. This delay is similar to the characteristics of the pitch response in hawkmoths (*M. sexta*), which displays a constant delay of 41 ms (Dyhr et al., 2013). However, the transfer function of the hawkmoths was found to be a first-order high-pass filter with a pass-band beginning at approximately 0.5 Hz, instead of a low-pass filter as inferred from our study. This could be due to the differences in the roles played by the abdomen in controlling flight in these two insects. Larger flying insects such as the hawkmoth may use pitch movements of the abdomen as an inertia-based means of rapidly altering (or regulating) pitch attitude during flight (Dyhr et al., 2013), whereas smaller fliers may change abdomen pitch to reduce drag. The latter does not require a fast controller, as the abdomen only needs to gradually adjust to the air speed (thus reflecting the response of a low-pass filter).

It is also possible that the abdomen’s role is multimodal, depending on the frequency and direction of movement of the image of the environment. For instance, our study has explored only low-frequency changes while subjecting the flies to a horizontally moving visual stimulus, while the experiments on hawkmoths by Dyhr et al. (2013) covered input frequencies of up to 20 Hz, but using a vertically oscillating visual stimulus. It is possible that abdomen movements play a streamlining role at low stimulus frequencies, and act to control or regulate pitch attitude at high stimulus frequencies, due to disturbances. Furthermore, changes in the speed of horizontal image motion would suggest that the insect is increasing or decreasing its flight speed, which would only require the abdomen to streamline its position gradually to maximise flight efficiency (after obtaining a reliable estimate of the new image velocity), whereas a change in the speed of vertical image motion (as in Dyhr et al., 2013) would require immediate attention for stabilising or redirecting flight in response to turbulence. Also, in comparison to the temporal response of hawkmoths, the pure delay in the abdomen pitch of the flies is approximately 8 ms longer (see Table 1), even though the flies possess a significantly higher wingbeat frequency (180 versus 25 Hz; Eberle et al., 2015). This suggests that the origin of the response latency may be in the visual

Table 1. The parameters determined for each transfer function in Fig. 7 along with the estimated accuracy of the transfer function to the obtained data

	K	a	b	c	τ	Fit error (%)
G11	0.048269	0.3913	0.03088	1.1777	0.048608	9.403
G12	0.044756	−20.86	0.3493	21.482	0.047846	12.83
G21	13.584	1.1445	0.0	1.6338	0.025807	10.68
G22	171.61	−13.201	0.0	98.558	0.0	17.26
G11+G21	—	—	—	—	—	14.65
G12+G22	—	—	—	—	—	23.76

Input–output combinations are as follows: G11: optic flow (OF) to abdomen pitch (AP); G12: OF to net thrust (NT); G21: air speed (AS) to AP; and G22: AS to NT. In the case of G21 and G22, one of the poles (described by the parameter b) was set to 0 and the transfer function was modelled as a first-order system, rather than a second-order system. The percentage error of the model’s predictions was assessed by calculating the magnitude of the difference in complex amplitude between the measured data and the model at each of the tested frequencies, and expressing the result as a percentage of the magnitude of the actual response.

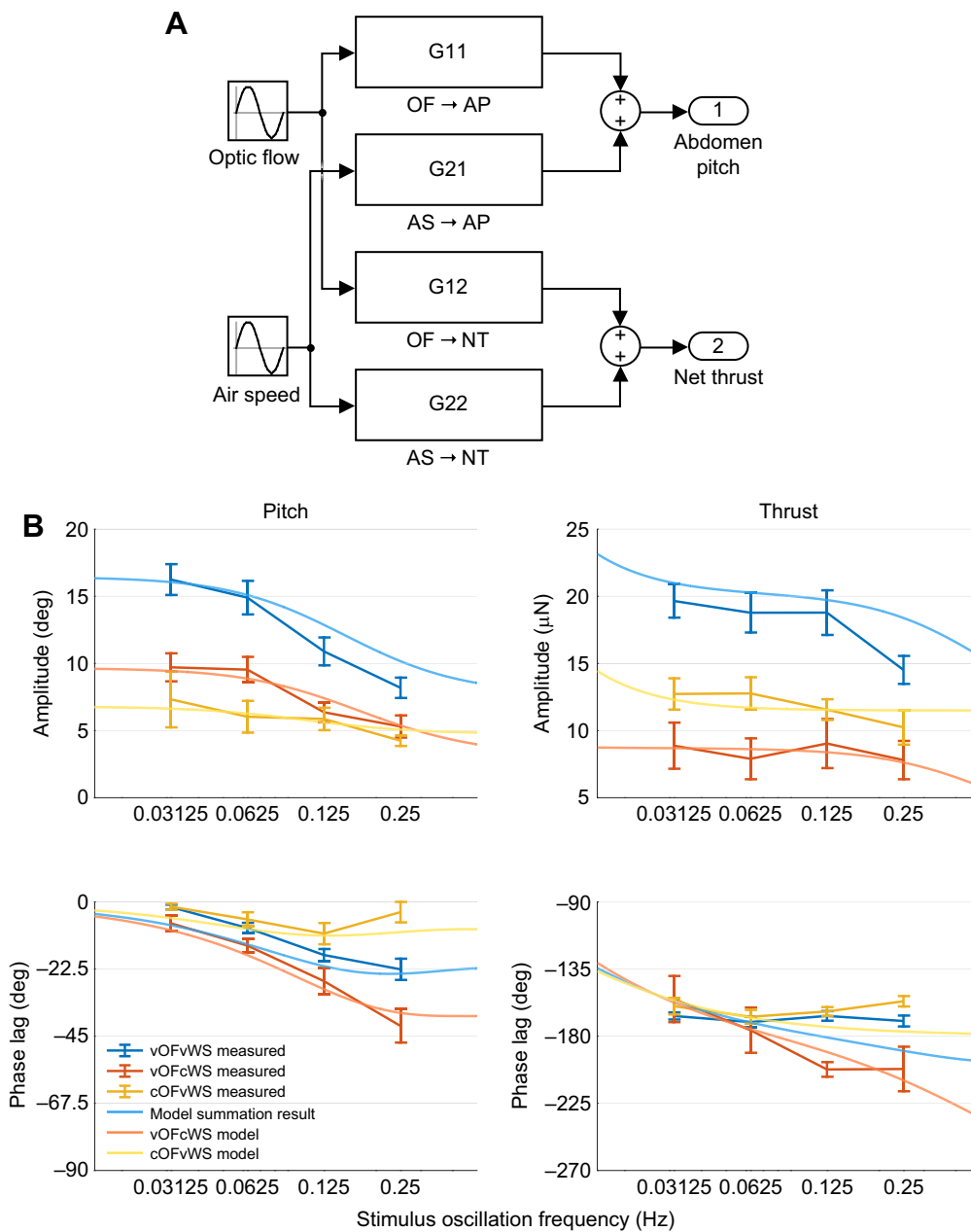


Fig. 7. A visual representation of the model and its theoretical outputs, compared against experimental results. (A) Block diagram model representing the open-loop abdomen pitch and net thrust controllers of the fly. (B) Comparison of theoretical response curves of the models against the actual responses measured. The transfer functions for each input–output combination [G11: optic flow (OF) to abdomen pitch (AP); G12: OF to net thrust (NT); G21: air speed (AS) to AP; and G22: AS to NT] are independent, and are summed with equal weights in the complex frequency domain to obtain the corresponding outputs. The forms of the transfer functions are as per Eqn 1.

processing pathway and not in the motor system. In our fruit flies, the amplitude of the abdomen pitch response decreases as the visual frequency increases, presumably because there is a physical limit to how fast the abdomen can move. The same effect is likely to be occurring in hawkmoths; however, in these insects, there could be an additional high-pass filter in cascade that improves the abdomen pitch response to high visual frequencies (caused by turbulence) and simultaneously suppresses the visual detection (and corrective stabilisation) of slower, intentional changes in pitch.

In contrast, a study by Whitehead et al. (2015) showed that *D. melanogaster* can initiate a pitch stabilisation locomotion (by wing-stroke modulation) in only 10 ± 2 ms, significantly faster than the results in the present study. This is also likely due to the different roles of the abdomen addressed earlier, as well as the fundamental differences in the responses of insects in free-flight versus tethered conditions (as the body orientation of the insect is not physically altered under tethered conditions).

The bimodal response characteristics observed in our counterphase experiments suggest that the flies sense the wind as well as the optic flow, but individual flies choose to respond preferentially to one stimulus or the other – displaying a form of selective attention, which needs to be studied further. However, another possibility is that the changes in drag force generated by the headwind experienced by some flies are significantly larger than the thrust generated, resulting in an inaccurate measure of the pure thrust generated by the fly. In future work, an infrared illumination system (such as that utilised in Götz, 1987) could be used to record the wingbeat amplitudes in real-time as a true measure of the fly's thrust, uncontaminated by wind-induced drag forces.

When the wind speed is modulated (i.e. in all experiments except for the constant wind speed experiments), there is an added passive effect to the net thrust measurements due to the wind pushing against the fly. Unfortunately, this passive effect is extremely close in phase with the natural thrust response of the fly (as speculated

from the optic flow modulation only experiments), which makes it difficult to isolate the thrust that the fly itself generates in response to the wind. For the purposes of our study, however, it is only the resultant force that is of interest, as this would be the force experienced by the fly during free flight if it was exposed to the same stimulus conditions. Also, in all successful flight experiments that registered an active thrust response, the net thrust measured by the force transducer was always greater than 0 during flight, signifying that the flight force generated by the fly was greater than the drag due to the wind at all times.

As shown in Table 1, the errors in the model fit for the thrust response (the outputs of the G12 and G22 filters, and their combined resultant) – at 12.83, 17.26 and 23.76%, respectively – are larger compared with the errors in the model fit for the abdomen pitch response (the outputs of the G11 and G21 filters, and their combined resultant) – at 14.65, 9.4 and 10.68%, respectively. This indicates that the thrust models describe the measured data consistently less accurately than the pitch response models. A reason for this reduced accuracy may be in the shape of the cOFvWS thrust phase response, where the phase lag stays constant, levels off or gradually decreases

after the initial increase, which does not coincide with standard filter behaviours. The decreasing phase lag may be due to measurement inaccuracies caused by the seemingly dominating passive wind effect on the thrust (as discussed above); however, it is also possible that the flies react in a nonlinear manner, where thrust control responsiveness increases with more rapidly changing environments.

It is clear from the transfer function parameters in Table 1, that for G21 and G22 (i.e. the transfer functions originating from air speed as an input), one of the pole constants, in particular b , was set to zero, to achieve a suitable fit to the data. This effectively reduces the transfer function to a first-order system with a comparatively slow response (compare the values of b and c for G21 and G22 with the corresponding values for G11 and G12 in Table 1). This development of the headwind handling system of the flies may have occurred because insects typically do not experience rapid changes in air speed (except during severe turbulence). Hence, the requirement would be for a stable controller, but not a fast response time. In contrast, optic-flow-based control would require a more agile system, given that insects can experience rapidly changing optic flow depending upon the environment through which they fly. The transfer function

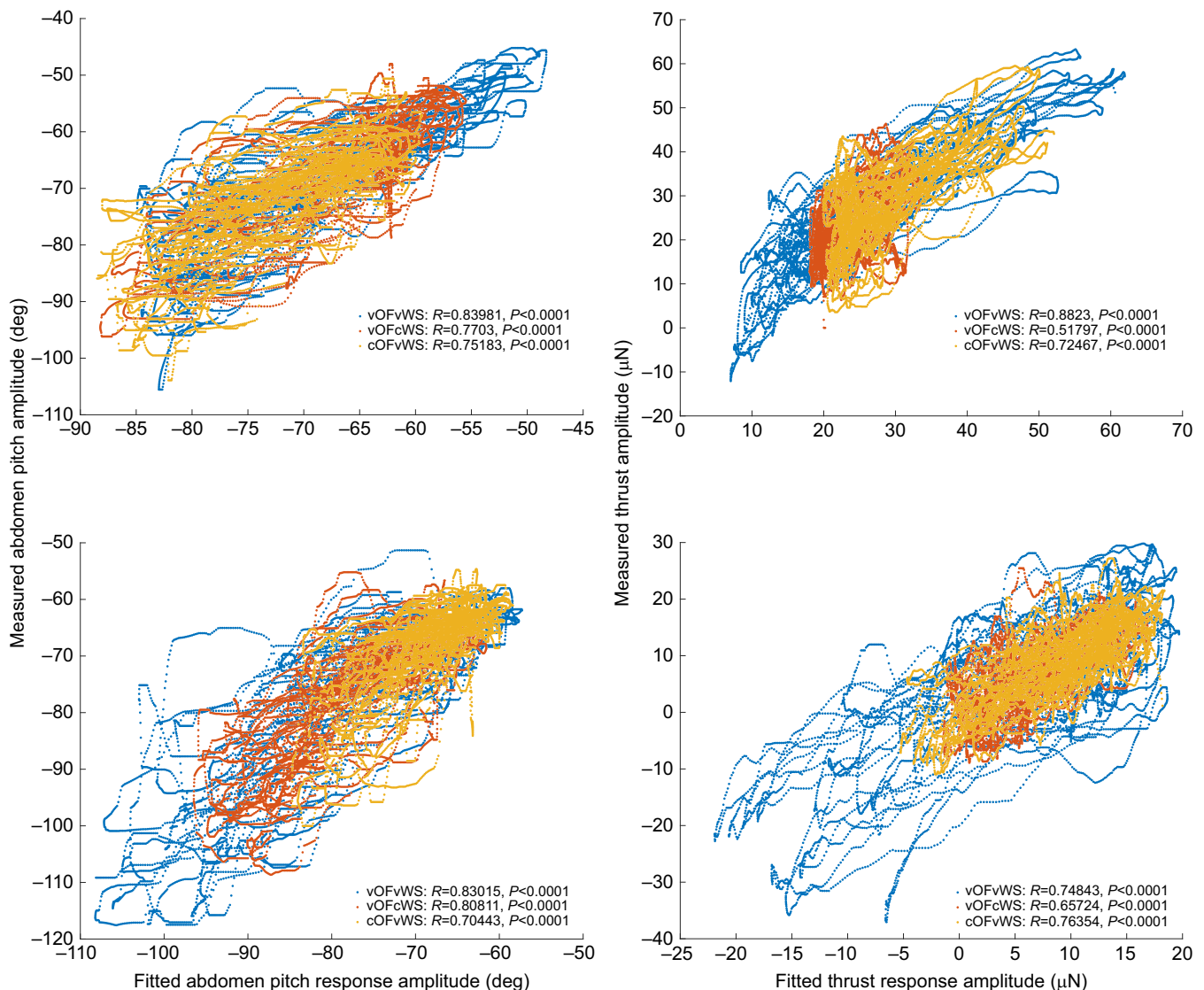


Fig. A1. Temporal correlation between the experimental measurements of the abdomen pitch and thrust and the predictions of the fitted model, plotted for two flies (top and bottom).

models also show that the pure time delay τ exhibited by the flies is in fact not the dominant cause of overall system lag, with noticeable effects only at the highest tested frequency.

A comparison of the model's responses with the measured data when both stimuli are oscillated in phase shows surprisingly accurate results in predicting the pitch response, as illustrated by the blue lines in Fig. 7B. When both the visual and wind stimuli are modulated in phase, the model predicts the pitch response to the stimulus combination accurately as the sum of the pitch responses to the individual stimuli, without the need to incorporate any arbitrary weighting factors to account for the relative contributions of the individual stimuli. In this experimental situation, the abdomen exhibited a streamlining response, where it was lifted with increasing stimulus magnitude (optic flow or air flow). However, the respective thrust responses do not superimpose in an exactly linear fashion. This could be related to the nonlinear behaviour observed in the cOFvWS experiments, or the fact that the observed passive wind effect could not be eliminated with the current apparatus for thrust measurement. From these results, we speculate that the internal flight controller weighs the visual and wind stimuli equally, without any preference, when the two stimuli vary in phase. However, when the inputs are in counterphase, a nonlinear phenomenon of 'selective attention' may determine the stimulus to which the fly responds.

APPENDIX

Dynamic response linearity

In order to confirm dynamic linearity of the stimuli to the flies' response, the correlation between measured and fitted responses of the increasing oscillation amplitude experiments was examined.

Fig. A1 shows the direct relationship between the fitted curve and the recorded outcomes of the pitch and thrust when the flies were exposed to sinusoidal stimuli with linearly increasing amplitude under three stimuli conditions.

Eqn A1 describes the linearly increasing sinusoid used for both stimuli:

$$S(t) = \left((A - b) \frac{t}{\tau} + b \right) \cos(2\pi ft) + c, \quad (\text{A1})$$

where b is the stimulus amplitude at the beginning of the stimulus exposure, A is the final stimulus amplitude at the end of the stimulus exposure [of duration (τ)], t is the time since the onset of the stimulus exposure, f is the frequency of the sinusoid in Hz and c is the baseline offset.

Step response comparison

To further validate our model, we recorded the thrust and abdomen pitch responses to a stimulus consisting of a concurrent step in wind and optic flow. This was done by recording the response at the beginning of each trial, when the wind and optic flow stimuli were turned on. The average step response of the flies was computed as the mean response measured over a time window extending from -1 to $+9$ s, where 0 s is the time of onset of the step stimuli. We analysed data from the vOFvWS case for the lowest tested frequency ($1/32$ Hz), using only flies that had commenced flight before the stimulus onset (in order to minimise artefacts caused by subsequent initiation of flight). The measured thrust and abdomen pitch responses were compared with the step responses predicted by the model. The results are shown in Fig. A2 for the pitch response and the thrust response. Both of the experimentally measured step responses display a slower rise time compared with the theoretical responses. This is likely due to the small lag in the onset of the wind stimulus, as the wind cannot be turned on instantaneously. The

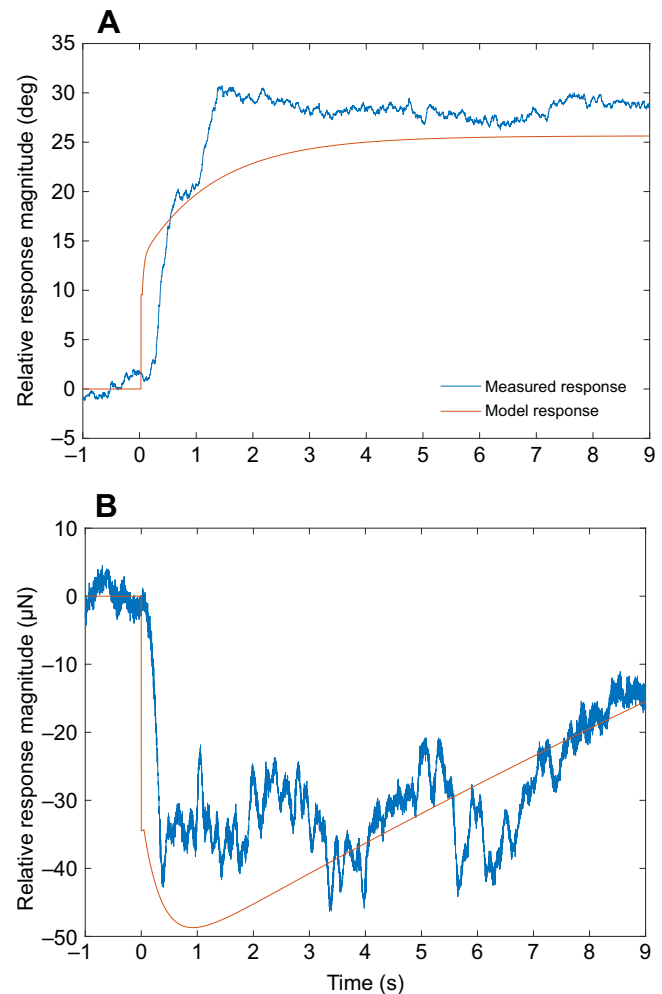


Fig. A2. Averaged step responses from stimulus initiation in vOFvWS flights, compared against predictions of the respective models. Measured and theoretical step responses of the abdomen pitch (A) and thrust (B) when the OF and wind stimuli are stepped simultaneously (OF: 0 to 450 deg s^{-1} and WS: 0 to 1.5 m s^{-1}).

measured pitch response exhibits a slightly larger steady-state value than does the model, which could be due to small errors in the estimation of the gain parameters (K) of the transfer functions listed in Table 1. Aside from these minor discrepancies, the measured step responses (pitch and thrust) are predicted reasonably accurately by the model, even though the model was derived using only sinusoidal stimuli. This correspondence between theory and experiment indicates that the observed pitch and thrust responses can be characterised reasonably well by linear dynamical models.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization, methodology, formal analysis, resources, writing – review & editing and funding acquisition: K.K.K.L. and M.V.S.; Software, validation,

investigation, data curation, writing – original draft, visualisation: K.K.K.L.; Supervision: M.V.S.

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