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An Information Theoretic Approach to Characterizing the Attention Shifts in the Fruit Fly During Flight

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FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

AN INFORMATION THEORETIC APPROACH TO CHARACTERIZING ATTENTION

SHIFTS OF THE FRUIT FLY DURING FLIGHT

A dissertation submitted in partial fulfillment of

the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

BIOLOGY

by

Nicholas Palermo

2021

To: Dean Michael R. Heithaus
    College of Arts, Sciences and Education

This dissertation, written by Nicholas Palermo, and entitled An Information Theoretic Approach to Characterizing Attention Shifts of the Fruit Fly During Flight, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this dissertation and recommend that it be approved.

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Date of Defense: June 22, 2021

The dissertation of Nicholas Palermo is approved.

                                 Dean Michael R. Heithaus
               College of Arts, Sciences and Education

                                        Andrés G. Gil
      Vice President for Research and Economic Development
          and Dean of the University Graduate School

Florida International University, 2021

DEDICATION

For my parents, who provided me with the opportunity to pursue the highest levels of my intellectual curiosity. For my partner, Diana, for always supporting me through even the most challenging moments of life. For my abuelos, who opened the doors to their home so that the burdens of life could not interfere with my goals. To Jeff: Somewhere in these pages is one of your ideas. I'm sure of it.

ACKNOWLEDGMENTS

ABSTRACT OF THE DISSERTATION

AN INFORMATION THEORETIC APPROACH TO CHARACTERIZING THE

ATTENTION SHIFTS OF THE FRUIT FLY DURING FLIGHT

by

Nicholas Palermo

Florida International University, 2021

Miami, Florida

Professor Jamie Theobald, Major Professor

To successfully navigate the complex visual world, animals must extract relevant information from the deluge of light-carried signals that arrive at their eyes. Early vision filters are passive, energy-saving gates that block out irrelevant signals and noise. The remaining incoming signals are then subject to active filtering by visual attention systems which are energetically expensive, especially for smaller animals, that are subject to similar survival challenges as larger animals.

Among visual behaviors performed by insects, flight stabilization demands one of the highest rates of information uptake. Flying insects must quickly respond to flight disturbances to avoid navigation errors and collisions. Active flight is energy-intensive, but the variable environmental and flight conditions make passive filtering unreliable to infer self-motion.

Dipterans (flies and mosquitos) are a prosperous order of insects that owe their success to impressive flying skills. Though many visual adaptations for flight have been well characterized, little research has been dedicated to the active attention processes required for flight stabilization. In this dissertation I investigated how the visual attention

systems of vinegar flies (herein referred to as "fruit flies") work to maximize relevant information uptake during flight. I have focused on three main questions: (1) Do flies shift attention away from regions affected heavily by motion-blur? (2) Do flies' attention systems prioritize regions with higher quality images? (3) Does the attention system only filter noisy regions or does it weigh the regional image quality against other sources of information present?

I used a virtual reality flight arena to convince stationary, tethered fruit flies that they were flying. I tested whether flies were attentive to visual regions by showing local perturbations and measuring corrective steering responses. I found that virtually fast-flying flies (1) shift their attention to the slower frontal parts of their visual field; (2) shift their attention forward when flying in dim and low contrast environments; (3) weight other relevant information against image clarity. My findings provide a better understanding of how the energy-limited visual systems of fruit flies can process all the information required to stabilize flight.

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PREFACE

Chapter II has been published in "Biology Letters" and is open access, so it can be

reproduced freely here for non-commercial purposes with the citations provided below.

The chapter has been formatted following the journal guidelines.

CHAPTER II

Palermo, N., & Theobald, J. (2019). Fruit flies increase attention to their frontal visual field during fast forward optic flow. *Biology Letters*, 15(1), 20180767.

CHAPTER I

INTRODUCTION

Animal visual systems need a great deal of information from the world. They handle many low-level tasks, such as detecting edges, computing lightness, perceiving motion, and estimating 3-D structure, as well as high-level tasks, such as navigating spaces, recognizing faces, and searching for objects (Jones et al., 1997). But the complexity of the visual world far exceeds the processing capabilities of any organism's brain (Tsotsos, 1990). Visual attention solves the problem of information saturation by narrowing stimuli to those that are likely relevant to the organism's current task (Niebur & Koch, 1998; Wolfe & Horowitz, 2004). Though it is well understood that attention serves to focus the processing of information that arrives at the brain, how the attention systems prioritize certain signals from the rest remains elusive.

Selective visual attention is often defined as the ability to focus visual processing to a smaller subset or region of the overall visual field (van Swinderen & Flores, 2007). Several theories have been developed to describe how the brain prioritizes one visual stimulus from a scene during selective attention. One of the most prominent theories is based on feature-integration theory which describes how bottom-up (preattentive) visual processes direct attention (Koch & Ullman, 1987). The basic premise is that when scanning a visual scene, the organism constructs 2D maps based on the features such as brightness, color, or motion (Treisman, 1980). The organism then integrates features to register individual objects that can then draw attention. The salience, or distinctiveness, of objects are then mapped by comparing their features to their surroundings (Itti et al., 1998). According to the models, the most salient objects, those that stand out most from their background, are prioritized (Fecteau & Munoz, 2006; Treisman, 1980). But quantifying the distinctiveness of objects is challenging.

"Image salience" is a term often used in the field of attention psychology but has been formally described in computational theories of bottom-up attention which have led to significant developments in computer-vision algorithms (Bruce & Tsotsos, 2009; Kadir & Brady, 2001). These models often describe salience with regard to information-based criteria, though they sometimes differ in which criteria they use (Bruce & Tsotsos, 2009; Findlay & Walker, 1999; Fritz et al., 2005; Kadir & Brady, 2001; Olshausen et al., 1993; Schmid & Mohr, 1997). But the general principle they share is considering salient regions that statistically differ from the background to have the highest Shannon-information content (Milanese, 1995; Shannon, 1984). The high Shannon-information content in these regions makes them inherently more useful for higher-level processing such as edge detection. The Shannon-information content of any probabilistic event quantifies the Shannon-entropy of the event, or how uncertain the outcome of an event is (Shannon, 1984). For example, revealing a future losing lottery number is not highly informative as it is nearly certain that any given number will lose. Revealing a winning number is, by comparison, a highly informative event. Therefore, selective attention systems assign high priority to visual regions that are unexpected and ignore those that are redundant.

The notion that bottom-up attention is guided, at least in part, by principles of information theory has been long known in human psychology literature (Attneave, 1954). Salient objects drive human overt (eye gaze) bottom-up attention (Foulsham & Underwood, 2008). But the extent to which these same principles of entropy and information content drive top-down (goal-directed) attention is still unknown.

Theories of top-down visual search tasks in humans describe the deep interplay between the bottom-up and top-down processes of visual attention (Sarter et al., 2001,

Wolfe, 1994). Bottom-up attention presents fast parallel-processing of streams of information which must then be acted upon by the slower serial-processing of top-down attention (Neisser, 1967). During a search, top-down attention systems search among salient (high entropy) objects mapped out by bottom-up attention processes (Wolfe, 2004). Much less is known about how bottom-up attention processes direct the top-down task of navigating through spaces.

Studies analyzing the human gaze during simulated driving, found that humans focus top-down attention on the tangential point (inflection point) of the inner road edge as it curves during a turn (Land & Horwood, 1995). As with any continuous line, the tangential point has the highest information entropy (Attneave, 1954). This point offers the most information about negotiating the curve (Boer, 1996). But we still don't know how information entropy contributes to the top-down attention processes during navigation in 3-dimensional space, without road edges.

Flying fruit flies (*Drosophila melanogaster)* rely on predictable patterns of visual motion over their entire visual field to assess their self-motion as they navigate through the environment. These optic flow fields and are unique for all translational or rotational motions (Gibson, 1950; Koenderink, 1986). Factors such as low scene brightness or low object contrast diminish the quality of optic flow fields by lowering the signal-to-noise ratio (SNR) of the self-motion signal, and therefore make it difficult to navigate (Warrant, 1999). But these challenging conditions don't affect all optic regions equally. For example during fast flight, visual regions orthogonal to the direction of motion have the fastest image speeds and therefore suffer the highest losses in image quality.

Flies use overt (head and body turning) and covert (mental shifting) attention to decide which part of their visual field to attend to while flying (Hengstenberg, 1993). I hypothesize that the covert attention systems of fruit flies prioritize those visual regions where they expect the highest information signals based on the spatial information capacity(H) of the eye in these regions. I describe H further in chapter III but, briefly, it is an entropy-based measure which describes how many unique scenes can ever be perceived by the eye in a visual region (A. W. Snyder et al., 1977). A high H region of the eye has more entropy since more unique scenes can be perceived in that region. An extreme example of a low H region would be one that only detects one of two possible inputs, depending on what it is viewing. This binary detector would only provide 1 bit of information. H, therefore, determines the information uptake rate of the eye in a given region. H limits the usefulness of visual regions because a region of low H cannot transmit high-information motion signals (A. Snyder, 1979).

I am interested in what regions of the eye flies have evolved to expect the most information-rich signals to arrive. Though often confounded with bottom-up attention processes in literature, *expectations* are top-down attention processes (Doshi & Trivedi, 2012; Summerfield & Egner, 2009). For example, the fly visual system can *expect* that faster-moving regions of the optic flow field provide less information, especially in a dim environment, and preemptively shift attention away to other regions.

The goal of my dissertation is to test whether these principles of information direct the covert attention of the fruit fly during a simulated flight in a virtual reality arena. Selective attention has been studied in insects, including dragonflies and honeybees (Wiederman & O'Carroll, 2013). But although fruit flies are a common model

for studying vision, surprisingly few studies have focused on flies' selective attention systems (Paulk et al., 2013). This deficit in research may be due to the difficulty of studying covert attention in insects, as a lack of response to a stimulus may result from decreased attention, or the inability to perceive the stimulus (van Swinderen, 2011). Using a virtual flight arena, I designed a protocol that measures when a fly fails to respond to a stimulus in a visual region that it can otherwise perceive under differing external conditions.

In chapter II, I test how simulated forward flight at different speeds affected the flies' visual attention to a steering stimulus. I describe the effects of increased image speeds on the Signal-to-Noise Ratio (SNR) of the visual field. I show that the reduced SNR due to the high image speeds caused flies to shift attention away to slower-moving regions. Chapter II has been published in *Biology Letters*.

In chapter III, I further expand on the ideas of chapter II by adding the effects of lower contrast and brightness. This chapter also introduces the *H* of eye regions, a more complex form of the SNR metric in chapter II, that considers the brightness, contrast, and spatial composition of the visual scenes. This chapter describes how flies use a similar attention-shifting strategy to compensate for the information loss in fast image regions when flying through dim and low contrast scenes. In this chapter, I also develop a model to determine which regions of the visual field provide the optimal H given the conditions of the visual environment and the fly's flight speed. This model generates testable predictions about the relative shifts in attention performed by flies.

In chapter IV, I describe one of the negative repercussions of shifting attention to determine why the flies do not always shift attention to higher H regions by default. If

attention shifts reduce usable visual field, flies' flight stability would suffer as optic flow

fields become increasingly ambiguous.

This dissertation will help guide future questions about the attention systems of

flying animals.

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CHAPTER II

FRUIT FLIES INCREASE ATTENTION TO THEIR FRONTAL VISUAL FIELD
DURING FAST FORWARD OPTIC FLOW

Nicholas Palermo and Jamie C. Theobald

Abstract

Flying fruit flies must compensate for the visual limitations of tiny compound eyes. The small apertures of each facet admit little light, and fast image motion during flight lowers light catch further still. Motion blur is especially problematic in the faster-motion regions of the visual field, perpendicular to the forward direction. We used a virtual reality flight arena to test whether fruit flies focus their attention on predictably slower regions of their visual field during simulated forward flight. We measured steering responses to pairings of simulated forward speeds with presentation angles of a stimulus to induce turning responses. We found that as forward speed increased, fruit flies responded more strongly to turning cues presented directly in front, and largely ignored cues presented out to the sides. Our results show that flying fruit flies shift their attention forward in response to high speed motion towards the periphery of their frontal vision.

Keywords: insect flight; optic flow; visual control

1. Background

The fruit fly, *Drosophila melanogaster*, is a passively unstable flier [1] and relies on vision to actively stabilize flight [2–5]. Flying flies continuously collect information about self-motion to adjust heading or counter unintended motion, such as lateral perturbations due to wind [6,7]. The usefulness of their visual field depends on the amount of information present in the scene, but is limited by the usable signal available (Figure 1A).

Rotation and translation produce characteristic patterns of motion over the entire visual field, and insects use these fields to stabilize flight [8,9]. For example, a translating

insect sees a focus of expansion in the direction of travel, motion away from this expansion throughout the visual field, and a focus of contraction behind [8,10]. Flow fields can be described by two-dimensional arrays of vectors representing image velocities in each part of a scene [10,11]. During forward translation, for example, the lowest image speeds are directly in front of and behind the insect (near the focuses of expansion and contraction) and the highest are perpendicular to the direction of travel (although actual image speeds are further reduced when objects are distant).

Motion speed affects the quality of retinal images [12]. Photon noise degrades all visual signals by some degree. This results from the quantum nature of light absorption, dictating that photons are absorbed only in discrete, random quantities that follow Poisson probability distributions, with variance equal to the mean [13,14]. In brighter light, therefore, noise (the standard deviation of mean absorption) increases only by the square root of light level [12,13]. In dimmer light, absolute noise is lower, but its relative contribution is higher [14,15]. The signal-to-noise ratio (SNR) is a good measure of how much useful information a signal contains [9,10]. Image SNRs decrease at both low luminance, when photons reflecting off objects in the environment are rare, and high image speeds, when objects reflect few photons onto the retina before leaving view [12].

Since regions of optic flow differ in speed, animals in challenging visual environments could rely on predictably slower regions for course correction and navigation, essentially shifting their attention to areas of higher SNR. Specifically, a forward-translating fly could reduce attention to its periphery and increase responsiveness to the slower images near its focus of expansion (Figure 1A, right side). To determine if flies use this

strategy, we monitored the corrective steering responses of tethered flying fruit flies in a visual flight arena, while simulating forward flow of different speeds, and lateral perturbations at different angles.
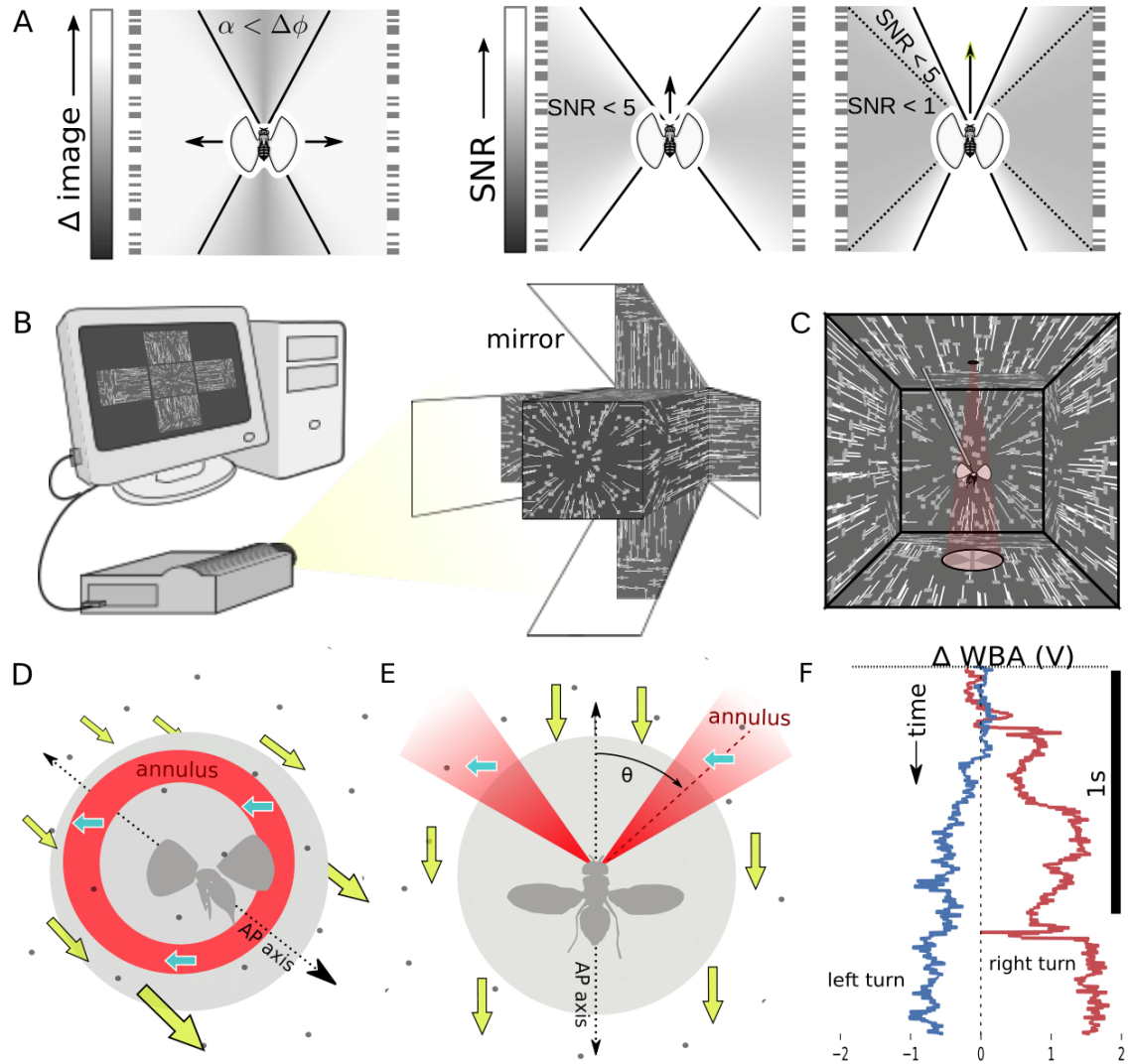
Figure 1 A *Illustrated top-down views of a fruit fly flying straight through a 10cm corridor with a high contrast pattern along its walls at dusk light levels. Leftmost figure shows the mean image displacements (Δ image) at azimuths around a fly that is laterally perturbed from its course by 2cm. Regions orthogonal to the fly's travel, especially the dorsal and ventral regions, where retinal images move a greater angular distance (α) than the interommatidial angle (Δφ) undergo the greatest image displacement. The two rightmost figures show the average signal-to-noise ratio (SNR) at different azimuths and how these ratios change in response to increased forward speed. The upward arrow length in-*

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*dicates speed. Angles with a SNR less than 1 and less than 5 (the Rose criterion) are demarcated. As forward velocity increases, the high SNR regions narrow around direction of travel. **B** Illustrates the computer-generated stimulus projected onto the five walls of the arena. **C** The view from inside the arena. The fly is immobilized to the arena's center. An overhead infrared light beam casts shadows over the wing beat sensor below. The tails on the dots are not rendered, but shown here to indicate motion. **D** Sample trial data showing differences in left and right wingbeat amplitude (ΔWBA) recorded over time. **E** Illustration of the visual area included in the sideslip annulus. The annulus area is the difference between two solid angles (here shown by their corresponding half-angles, θ_1 and θ_2) centered about the point directly in front of the fly.*

2. Methods

Subjects and preparation

Drosophila melanogaster were raised in an incubator on a standard food medium and maintained on a 16h:8h light:dark cycle. Female flies were collected 4-6 days after eclosion. We cold-anesthetized flies and tethered them to a 0.1mm tungsten rod by the dorsal prothorax, then allowed at least an hour at room temperature for recovery. We then suspended them in the center of a virtual arena (Figure 1B) for testing. Each of the 50 flies participated only once under each experimental condition.

Steering responses

Drosophila respond to visual stimuli by adjusting the relative amplitudes of their left and right wingbeats [6]. We measured steering responses with an infrared light emitter above the fly, and sensor pair below. A wing beat analyzer recorded the wing shadows, giving estimates of each wing beat amplitude (WBA) based on sensor occlusion. The right WBA subtracted from the left gives ΔWBA, a measure which correlates with steering yaw torque (figure 1D) [17,18].

Visual Stimuli

The virtual arena was a perspex cube with 200mm edges and the rear face missing for researcher access. A projector and mirrors displayed images simultaneously on the 5 faces, covering the front 5/6 of the visual field (figure 1B and C).

We displayed 12 open-loop 4.5s trials, with 2.5s rest between each. During the rests, flies controlled the angle of a vertical stripe in closed-loop, which active, healthy flies tend to fixate in front. Stripe fixation motivates flies to continue participation, and ensures they entered each experiment in an active tracking behavioral state. Ability to fixate the stripe was the only inclusion criterion used. During trials, the projector displayed a field of dots in a uniform random distribution throughout the visual space. The dots were divided into two regions based on their visual angle. One annular (ring-shaped) region was defined by the edges of a spherical segment centered directly in front of the fly (figure 1E). This annulus always covered 25% of the entire visual arena area regardless of its position, meaning that at larger angles the annulus was thinner. The second region consisted of all visual area outside the annulus, the remaining 75% of the arena. Dot motion was perspective corrected, so virtually distant dots moved slower. Dotsfrom either of the two regions never overlapped, even if a point's motion would cause it to do so. Instead, a point leaving one region due to their own motion became invisible during transit through the other region.

During trials, all dots outside the annulus moved to simulate forward translation, from the focus of expansion, around the fly and behind. We simulated three forward speeds, corresponding to mean angular speed of dots perpendicular to the fly of, 0.00

rad/s (no FF), 0.76π rad/s (slow FF), and 1.52π rad/s (fast FF). Dots inside the annulus, in contrast, moved laterally to simulate sideslip, following a 0.44hz triangle wave, the only lateral steering cue presented to the fly. For flying fruit flies, visual sideslip produces a strong corrective steering response [19].The annulus took on one of four non-overlapping positions per trial, with boundaries of 0, 0.58π, 0.85π, 1.09π, and 1.35π radians from forward taken as subsequent pairs. For testing, each of the three forward velocities was paired with each annulus position for a total of 12 trials. The time series of each fly's ΔWBA response was cross-correlated to the sideslip motion of the annulus dots. Paired t-tests then compared the mean correlations across experimental conditions.

3. Results
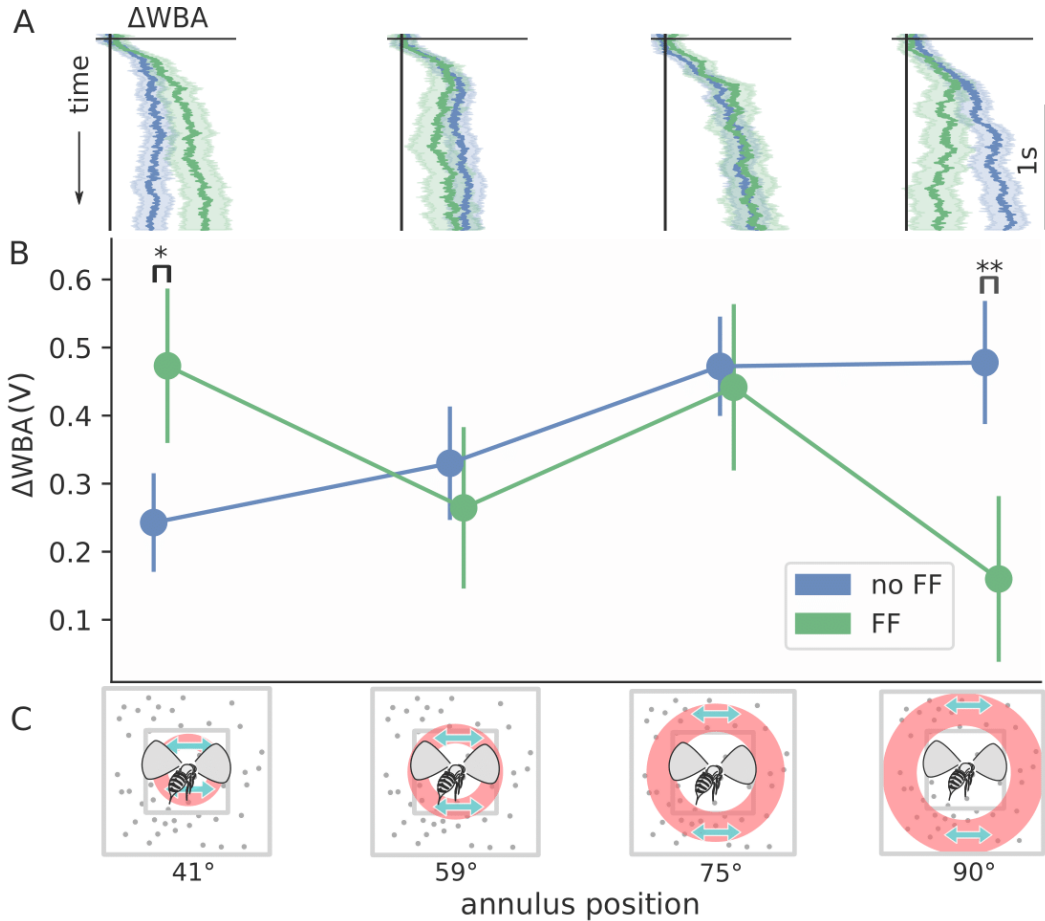
Figure 2 *Steering responses depend on visual angle of the cue* ***A*** *The mean responses across trials for each experimental condition with standard error shaded (n = 50). Leftmost black trace shows the annular lateral motion.* ***B*** *Cross correlations between ΔWBA responses with the lateral motion of the annulus dots at each presentation angle (written as a range of half-angles from forward) and forward flow velocity (FF). Asterisks indicate paired t-test significance of P < 0.05 (single) and P < 0.005 (double).*

The lateral dot flow, even restricted to the small visual regions of the annuli, induced steering responses that corresponded to its motion (Figure 2A). With no forward flow, flies respond to lateral cues originating forward or to the side, slightly favoring forward cues. But flies made significantly stronger corrective responses to the most anterior presentation of the sideslip annulus, the forward annulus (0.00π rad – 0.29π rad range), as the FF dot field velocity increased (Figure 2B). (p<0.005 for fast FF> no FF, p<0.005 for

slow FF> no FF, p<0.05 for fast FF > slow FF). Responses at the other annuli presentations did not show significant differences between the FF velocities, although there is a consistent decrease in response to the lateral annuli during fast forward flow.

4. Discussion

During forward flight, visual regions with the greatest image speeds are typically perpendicular to the flight path and therefore suffer from the greatest motion blur. Our results suggest flies shift attention forward to counteract the effects of increased motion blur. This attentional shift did not depend on the actual presence of motion blur, since our sideslip stimulus had no forward velocity.

For these experiments, regions simulating forward flow and regions simulating sideslip were separate, meaning the forward flow regions affected responses to regions absent of forward flow. Putting forward flow everywhere would have added a confounding variable, angular speed, to the perception of sideslip. However pilot experiments with this compound stimulus indicate similar results to those reported here. It remains unknown if this strategy could generalize to motion in other directions. Typical flight bouts for fruit flies are composed of longer periods of forward translation punctuated by rapid turns [20]. The heavy reliance on forward translation may have resulted in attention shifting that is hard-wired only for forward flight. The forward shift also suggests some value in using peripheral visual regions for sideslip corrections, otherwise flies might rely only on forward regions regardless of flow speed. This may reflect the higher visual displacement during sideslip in the peripheral regions as an insect passes nearby environmental features (figure 1A, left). Previous work has shown flies spatially blur in peripheral regions during forward flow, consistent with neural summation that improves SNR at the

cost of acuity [21]. Further, flies shift attention to different regions when responding to translational and rotational motions, as they produce different image speeds on the retina [22].

Flight speed is not the only factor that can reduce the visual SNR. Diminished light intensity, eye size, or image contrast, could similarly make regions near the focus of expansion more useful for flight stabilization. Small flies face many challenges in executing competent flight, and attentional shifts may be one mechanism helping to maximize their information uptake.

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CHAPTER III

IN DIM LIGHT OR LOW CONTRAST, FLYING FRUIT FLIES RELY ON
SLOWER REGIONS OF THEIR OPTIC FLOW FIELD

Abstract

To achieve robust natural flight performance, fruit flies must extract information about their intended and actual track from intricate visual scenes. But natural environments can make this already difficult task harder, such as when light is insufficient, or objects provide poor contrast against the background, or image motion blurs features that sweep quickly over the retina. If animals can identify and analyze image regions that minimize these problems, they might improve visual confidence. Forward motion provides a somewhat predictable optic flow field, with fast image flow to the sides, perpendicular to motion, and stable points of expansion and contraction in front and behind. We speculated that *Drosophila* flying with challenging visual scenes might shift attention to regions likely to move more slowly and tested this hypothesis by measuring wingbeat responses to identical steering cues. We find flies steering under dim light or poor contrast shift attention to forward, slower moving visual regions, which improves visual reliability at the cost of representing potentially more distant, less immediately relevant environmental objects. Flies may use this neural strategy to regain image contrast by minimizing motion blur whenever image statistics become unfavorable during flight.

Table 1: List of important symbols

n_d	= light detector density measured as the number of light detectors per square radian
n_i	= number of perceived light intensities per detector
H	= spatial information capacity of an eye or eye region
C	= average scene contrast
I	= average scene intensity in lux
I_t	= intensity modifier due to image velocity

M = modulation transfer function of the eye in the spatial domain

Φ = receptive angle of a light detector or ommatidia, 5° for *Drosophila melanogaster*

vdt = mean angular velocity of the scene measured in radians per integration time

r = distance to an object in m

θ = inclination angle in radians measured from directly in front of the fly

V_f = forward speed of the fly in m/s

1. Introduction
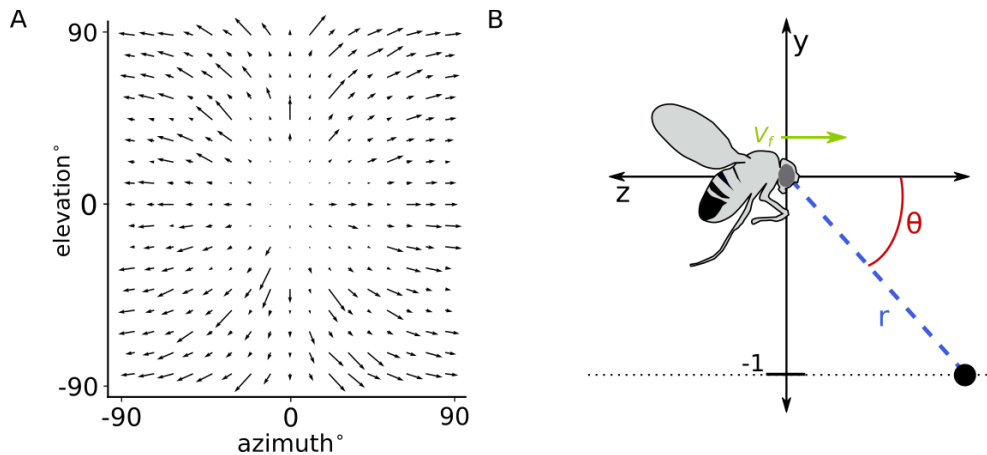
Figure 1 (A) Frontal half of the flow field experienced by a forward moving fly in a space filled with randomly placed dots. The vector lengths describe the image speed at each elevation and azimuth angle. (B) In the model, θ is the inclination angle from the z-axis to the object. The fly is oriented facing the positive z direction. r is the distance from the fly to the object. All objects in the model are at y=-1m.

Vision provides light-carried information about objects in the real world (Fellgett & Linfoot, 1955), but natural scenes are too complex for organisms to fully process in real time (Tsotsos, 1990). Filtering and attentional mechanisms can reduce the computational strain on visual systems by allowing them to rely on only a subset of a scene (Tsotsos, 1997; Wolfe & Horowitz, 2004), but even among pre-filtered stimuli, some have more predictive power than others for a given task (Geisler, 2008). To take

advantage of this, an organism might prioritize visual elements likely to provide the maximal relevant information.

The distribution of light intensities arriving at an eye from different angles of a scene is the spatial information of that scene (Fellgett & Linfoot, 1955). The spatial information capacity (H), of the eye (or camera) gives us an understanding of its picture-making abilities (A. Snyder, 1979). Specifically, H describes how well the eye can assign unique intensity values to light from each incoming angle. H is an entropy calculation which estimates how many unique images the eye can resolve (A. W. Snyder et al., 1977).

In its most general form:

$$H = n_d \cdot \ln(n_i) \tag{1}$$

where n_d is the number of individual light detector subunits that make up the retina of the eye and n_i is the number of discernible light intensities that can be assigned by each detector. Therefore, an eye composed of detectors with poor abilities to differentiate between light intensities has a low H. Though poor intensity discrimination can be due to intrinsic factors such as a detector's tolerance to thermal and transducer noise (Barlow, 1956; Denton & Pirenne, 1954; Howard & Snyder, 1983) the image source also provides limits to H that result from extrinsic noise (Rose, 1953; A. W. Snyder et al., 1977). For example, due to the quantum nature of light, in dim conditions, the variance in photons arriving at a detector is relatively large compared to the mean number of photons absorbed by the detector so distinguishing light levels becomes difficult (Howard &

Snyder, 1983; Rose, 1953; Warrant, 1999). An eye that can form images perfectly well in bright conditions may instead have difficulty when photon counts are low.

The individual light detecting subunits of the insect compound eye are called ommatidia. The number of discernible light intensities that each ommatidia can detect in a scene is modeled by:

$$n_i = \ln\sqrt{C^2 \cdot I \cdot M + 1} \tag{2}$$

Where C is the mean contrast of the scene, I is the mean intensity of the scene, and M is the modulation transfer function which defines the insect eye optics' contrast sensitivity at different spatial frequencies (A. Snyder, 1979; Warrant, 1999). Following this equation, H decreases in both dim lighting and low contrast environments.

The effect of increasing image speed is similar to that of dimming the visual scene since it also reduces the number of detected photons per integration time unit of the detector (A. Snyder, 1979). I in equation 2 therefore reduces by a factor I_t:

$$I_t = e^{(-1.78)\frac{vdt^2}{\Phi}} \tag{3}$$

where vdt is the angular speed of the scene's images per integration time unit and Φ is the receptive angle of the detector. Therefore, for detectors observing moving images:

$$n_i = \ln(\sqrt{C^2 \cdot I \cdot I_t \cdot M + 1}) \tag{4}$$

Substituting equation 4 into equation 1 and replacing n_d with the reciprocal of Φ^2 :

$$H = \frac{\ln(C^2 \cdot I \cdot I_t \cdot M + 1)}{2\Phi^2} \qquad (5)$$

Therefore, n_i and consequently H, decrease at fast image speeds.

The fruit fly, *Drosophila melanogaster*, is a passively unstable flier and depends heavily on its vision to stabilize flight (Smith, 1952). It uses motion cues from optic flow fields to detect perturbations and correct for the unintended motion (Borst & Haag, 2002; Combes & Dudley, 2009; Götz, 1968). Optic flow fields are described by two-dimensional vector maps which show the local image velocity of points over the entire visual field (Koenderink & van Doorn, 1987; Nakayama & Loomis, 1974). These flow fields have predictable patterns during flight translations and rotations, which makes them ideal for quickly and accurately assessing self-motion.

Optic flow fields can have large disparities in image speeds throughout their surface. For example, a forward moving fly experiences a flow field with frequently relatively low image speeds in front near the point of expansion, compared to regions orthogonal to their flight trajectory (figure 1A). The orthogonally-directed regions of the eye should therefore experience significant reductions in H. Given that H can vary significantly throughout a flow field, we simulated how the brightness, contrast, and flight velocity can affect the regional H of the fruit fly eye.

The optical design and neural arrangement of insects' eyes maximize H in accordance with each insect's normal flight speed and flight conditions (A. W. Snyder et al., 1977). The rapid adaptations of the insect eye under environmental constraints also

maximize H by increasing the number of perceived light intensities by visual channels (Laughlin & Hardie, 1978; Warrant, 1999). We propose that visual attention during a navigation task is another method by which insect visual systems work to maximize H.

Fruit flies experience forward optic flow during a large majority of their time flying (van Breugel & Dickinson, 2012)**.** To maximize spatial information while experiencing these forward optic flow-fields, a fly might shift its attention to the slower moving portions in its frontal field with higher H. Fruit flies have already been shown to shift attention forward during a simulated fast flight (Palermo & Theobald, 2019). Here we wish to test whether fruit flies also use this same strategy to recover lost H during fast forward flight in low contrast and low brightness conditions. We would expect interactions between brightness, contrast, and image speed so that at faster forward speeds, dimmer brightnesses, and lower contrasts, the fly's forward attention shifts would be more prominent. We tested the strength of *Drosophila melanogaster* forward attention shifts under these varying image conditions in a virtual flight arena.

2. Methods

2.1 Simulating the effects of forward velocity, scene contrast, and scene brightness on regional H for a flying fruit fly

We can calculate the theoretical H of eye regions of a forward moving fruit fly by determining the angular image speeds of objects in those regions. We will calculate the angular image speeds for the 2-dimensional case like Lingenfelter et al. (2020). To calculate the angular image speeds at each region we first need to assign an inclination angle(θ) and distance(r) to objects in the 3D world relative to the fly's head:

$$r = \sqrt{y^2 + z^2}$$

$$\theta = \cos^{-1}\left(\frac{z}{r}\right) = \tan^{-1}\left(\frac{y}{z}\right)$$

Where θ is measured from a point directly in front of the fly. y and z are the distances the object is along each axis (figure 1B). We will also set the upper limit of θ to $\pi/2$, and only consider the front half of the fly's visual field. We calculate the time derivatives of θ with the chain rule:

$$\frac{d\theta}{dt} = \frac{z\frac{dr}{dt} - r\frac{dz}{dt}}{r^2\sqrt{1 - \left(\frac{z}{r}\right)^2}} = \frac{z\frac{dr}{dt} - r\frac{dz}{dt}}{r^2\sqrt{1 - \cos^2(\theta)}} = \frac{z\frac{dr}{dt} - r\frac{dz}{dt}}{r^2\sin(\theta)}$$

$$\frac{dr}{dt} = \frac{y\frac{dy}{dt} + z\frac{dz}{dt}}{r}$$

Because our fly moves only in the forward direction, dy/dt is 0 and dz/dt is the negative of the fly's forward velocity (V_f). Therefore:

$$\frac{dr}{dt} = \frac{z}{r}\frac{dz}{dt}$$

$$\frac{d\theta}{dt} = -V_f \cdot \frac{\frac{z^2}{r} - r}{r^2\sin(\theta)}$$

30

Because for many animals in real flight, the ground provides the most reliable source of translational optic flow, we will simplify the model and restrict it to objects 1 meter below the fly's altitude (y=-1).

$$z = \frac{-1}{\tan(\theta)}$$

$$r = \sqrt{1 + z^2} = \sqrt{\frac{1 + \tan^2(\theta)}{\tan^2(\theta)}} = csc(\theta)$$

$$\frac{d\theta}{dt} = -V_f \cdot \frac{\frac{cot^2(\theta)}{csc(\theta)} - csc(\theta)}{csc^2(\theta)\sin(\theta)} = -V_f sin^2(\theta)$$

Therefore, the fly experiences image speeds that only depend on its flight speed and the object's angular position from the forward direction (θ). To calculate the angular image displacement in one integration time ($v\varDelta t$) we will use 21ms for the integration time since it is the peak time of the temporal delay kernel found in *Drosophila melanogaster* motion detectors (Harris et al., 1999).

$$v\varDelta t = -0.021V_f sin^2(\theta)$$

Substituting this $v\Delta t$ into equation 3 gives:

$$I_t = e^{-1.78\frac{(-0.021 V_f)^2 \cdot \sin^4(\theta)}{\Phi^2}}$$

$$(6)$$

where $\Phi = 5°$ for *Drosophila melanogaster*. Figure 2A shows the effects of V_f on I_t for an object located orthogonally ($\theta = \pi/2$) and an object located frontally ($\theta = \pi/5$). I_t drops significantly for objects orthogonal to the fly compared to frontally located objects as V_f speed increases. Given the scene C and I along with V_f we can then calculate H at any θ by substituting I_t from equation 6 into equation 5:

$$H(\theta) = \frac{\ln(C^2 \cdot I \cdot M \cdot e^{-1.78\frac{(-0.021 V_f)^2 \cdot \sin^4(\theta)}{\Phi^2}} + 1)}{2\Phi^2}$$

$$(7)$$

To reduce the complexity of the model we will assume the fly sees all spatial frequencies of the image spectrum equally well and set M to 1.

2.2 Attention Experiments
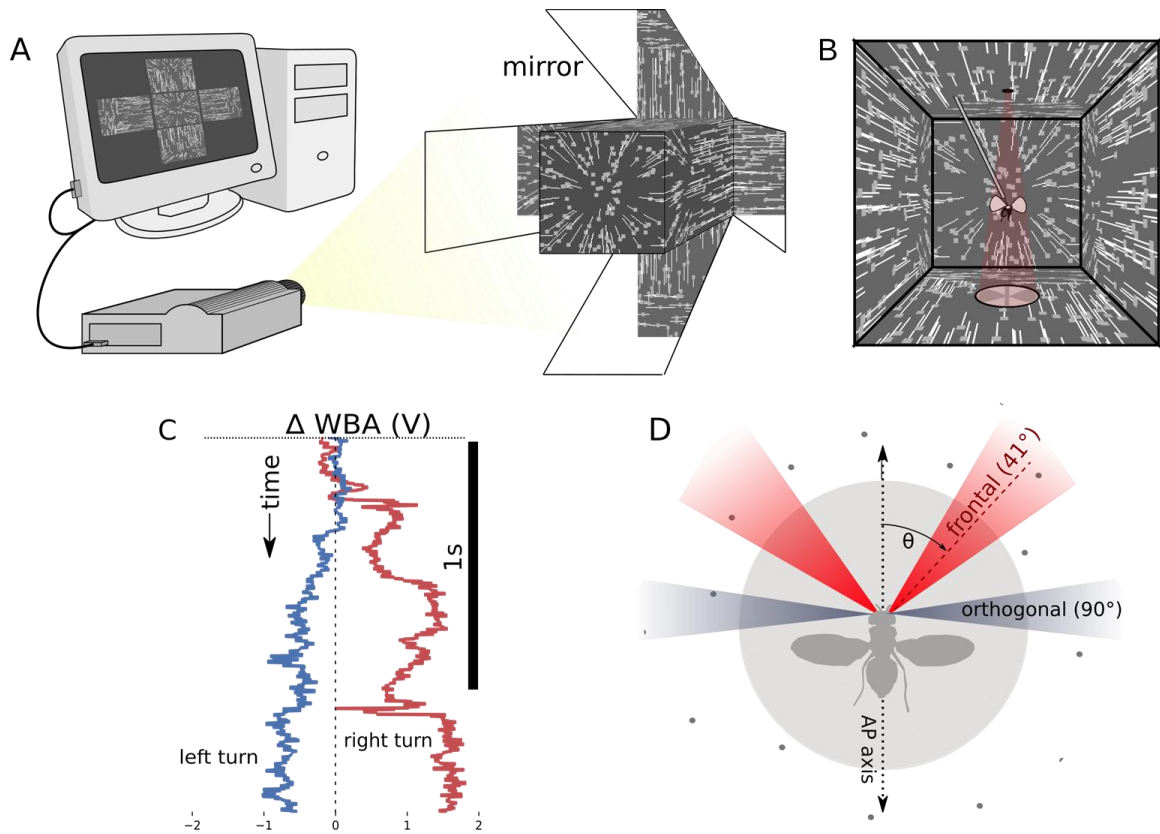
Figure 2 (A) Computer-generated visual stimuli projected onto the virtual reality arena. (B) Interior of the arena. The fly is mounted in the arena's center with infrared emitter above and sensor below. (C) Sample trial data recorded from an individual fly. Changes in left minus right wingbeat amplitude (ΔWBA) recorded voltages shown during a left and a right attempted turn. (D) Top-down diagram showing frontal and orthogonal annulus positions that were tested.

2.2.1 Virtual Arena

The virtual arena was a cube assembled from acrylic sheets with edges 200mm long. The rear wall of the cube is missing so that researchers could access the inside. A modified DepthQ WXGA-360 projector and four mirrors were set up so that 5 faces of the cube could be projected onto simultaneously (figure 2A).

2.2.2 Experimental Subjects and Preparation

We reared female *Drosophila melanogaster* on standard food medium, maintained on a 16h:8h light:dark cycle, and collected them 4-6 days after eclosion. We cold-anesthetized the flies and tethered them to a 0.1mm tungsten rod. They recovered at room temperature for at least an hour. We suspended flies in the center of a virtual flight arena in a natural flight body position for testing (figure 2B). During preparation and testing, we dimmed the room lights. Flies were dark-adapted in the room for at least 15 minutes before testing. For each experiment, flies performed all trials only once.

2.2.3 Visual stimuli

For each experiment, flies were presented 1.2 second trials in a randomized order with a 2.5 second rest between each trial. During the rest period, flies controlled the angle of a vertical white bar in closed-loop. Flies fixate on vertical stripes and center them directly in front (Heisenberg & Wolf, 1979; Reichardt & Wenking, 1969). The ability to center the bar was the only inclusion criteria used for the experiments. Data during rest periods were not analyzed. The stimulus used in every experiment was a projected 3-dimensional field of dots in a uniform random distribution around the fly (dot density of 16.6 dots/steradian). The dot field was perspective corrected so that closer translating dots moved faster than those that were further away.

To test attention shifting we used a protocol similar to Palermo & Theobald (2019). A region of the dot-field was used to elicit steering responses. This region was a conic ring-shaped volume, an "annulus", centered about the antero-posterior (AP) axis of the fly which was set to cover either the frontal or lateral portion of its visual field. The

annulus's volume demarcated a subgroup of dots which only translated laterally in one direction (leftward or rightward), providing the fly with a steering cue. The annulus always covered 26% of the projection area, and was thinner in the lateral position to compensate for its increased diameter. The frontal and orthogonal annuli covered the visual regions centered at 41 and 90 degrees from the AP axis (figure 2D).

During trials, all dots outside the boundaries of the steering annulus were translated from the front of the arena towards the rear to simulate the visual optic flow a fly would experience during forward flight (FF). The speed of these FF dots varied depending on the conditions of the individual trial. To facilitate discussion, all dot speeds in this article will be presented as the mean angular speed of a full field of dots as they pass their fastest portion of the visual field. For example, FF dots would have the highest angular speed along the fly's transverse plane, so FF speeds will be presented as the mean angular speed of dots passing the transverse plane. For laterally moving dots, the highest angular speed would be along the fly's midsagittal plane, which is reported.

Dots located in the annulus were always laterally translated at a speed of 0.37π rad/s, to simulate sideslip, though virtually closer dots had higher angular speeds while virtually farther dots moved slower. All conditions were tested with both leftward and rightward annulus dot motions. Dots disappeared as they left the boundaries of the annulus, and new dots replaced them on the opposite side. The FF dots outside the annulus disappeared as they traversed through the annulus then reappeared once they exited. Flies make corrective steering maneuvers in response to the lateral motion of points in the annulus (Palermo & Theobald, 2019).

2.2.4 Steering responses

Flying *Drosophila* steer by adjusting the relative amplitudes of their left and right wingbeats. We measured amplitudes with an infrared(IR) emitter and detector pair above and below the fly (figure 2B). The detector reported wingbeat shadows as voltages, then converted to wingbeat amplitudes (WBA). We subtracted right and left WBAs to compute ΔWBA which correlates to steering yaw torque. Positive ΔWBA shows attempted right turns and negative values show attempted left turns (figure 2C) (Tammero et al., 2004). The last 500ms of each trial were averaged to get the mean ΔWBA for each trial. Each experimental condition was tested with leftward and rightward motion then sign-adjusted so steering with motion was considered positive. We tested responses to the annulus at two positions, frontal and orthogonal, and with two directions, left and right, yeilding four trials per experimental condition.

The relative frontal response (*RFR*) was measured taking the difference of the ΔWBA for the frontally located annulus responses (ΔWBA_{front}) and the orthogonal annulus responses (ΔWBA_{orth}) then dividing by their sum:

$$RFR = \frac{\Delta WBA_{front} - \Delta WBA_{orth}}{\Delta WBA_{front} + \Delta WBA_{orth}}$$

A positive RFR near 1 implies a fly responded more strongly to the annulus in the frontal position. A RFR near -1 implies a stronger response to the orthogonal annulus. A RFR near zero implies equal response to frontal and orthogonal annuli.

The sign of RFR should only come from the numerator term. Flies do not typically countersteer in our trials, so ΔWBA and sums of ΔWBA from frontal and orthogonal trials are almost always positive. But for occasional cases when the sum of ΔWBA was negative, the denominator of RFR would affect the sign of the RFR and therefore would make RFR results unreliable. To account for this issue, when flies responded with a negative ΔWBA for any trial, the ΔWBA for all of that fly's trials were increased by the same amount so that the previously negative trial's ΔWBA value was instead zero. We also provide figures showing the raw ΔWBA_{front} and ΔWBA_{orth} before adjustments were made in the results.

2.2.5 Effects of brightness on RFR

We used a multi-factorial design to test the effects of decreasing brightness on regional responsiveness during FF. A neutral density filter (NDF) located in front of the projector controlled the brightness while maintaining equal contrast. All brightness experiments maintained a mean contrast of 0.99, measured as the difference between the intensity of the dots and the background divided by their sum.

We recorded steering responses (ΔWBA) to the orthogonal and frontal annuli at five different NDF settings corresponding to brightness levels 6.1, 7.0, 7.5, 7.9, 8.5 lux and two FF speeds (mean angular speed: 0.00π rad/s and 0.37π rad/s). The five brightness levels, two FF speeds, two directions of sideslip, and two annulus positions resulted in 40 conditions for each trial. We tested 28 flies in this experiment.

2.2.6 Effects of contrast on RFR

We used a similar arrangement to test increasing contrasts on regional responsiveness by altering foreground and background intensities of the dot-field. All trials in the contrast experiments maintained approximately constant overall brightness of 32.1 lux.

In this experiment, we recorded the flies' responses to the annuli at both positions at four different contrasts (0.82, 0.92, 0.97, 0.99) while paired with two FF dot speeds (0.00 and 0.18π rad/s). The two contrasts, four speeds, two directions of sideslip, and two annulus positions resulted in 32 conditions each. We tested 32 flies in this experiment.

We also performed another arrangement of the previous contrast experiment with 2 contrasts (0.82 and 0.99) and 4 FF dot speeds (0.00, 0.06π, 0.12π, 0.18π rad/s). We tested 31 flies in this experiment.
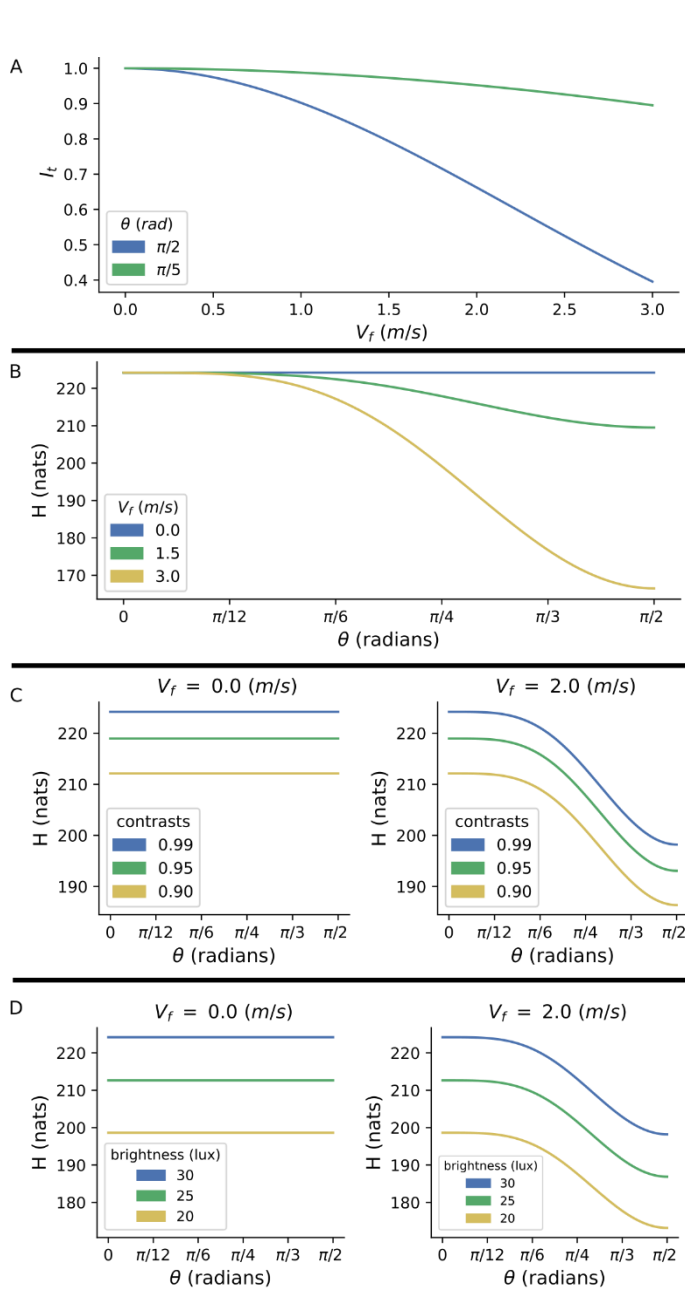
Figure 3. Calculations from the model showing regional H at different C, V_f and I. (A) The relationship between the light intensity modifier, I_t, and the fly's forward flight speed, V_f. The calculations are shown for an orthogonally located object ($\theta=\pi/2$) and a frontally located object ($\theta=\pi/5$). (B) The relationship between H and θ of an object at 3 different flight speeds. I was set to 30 lux and C was set to 0.99. (C) The relationship between H and the θ of an object at 3 different C. The calculations are shown for a stationary fly and a fly flying at 2.0 m/s. (D) The relationship between H and the θ of an object at 3 different I. The calculations are shown for a stationary fly and a fly flying at 2.0.

3. Results

3.1 Simulation calculations

Due to the decreased I_t in the orthogonal regions during fast forward flight, these regions are dimmer and have reduced *H* (Figure 3B). When the fly is stationary, *H* is consistent across all θ. For both stationary and moving conditions, reduced *C* results in decreased *H* across all θ (Figure 3C). But in the moving condition, *H* is decreased even further in the orthogonal regions. Similar effects occur when *I* is reduced (figure 3D).

3.2 Flies rely more heavily on the frontal region when flying in dimmer environments.
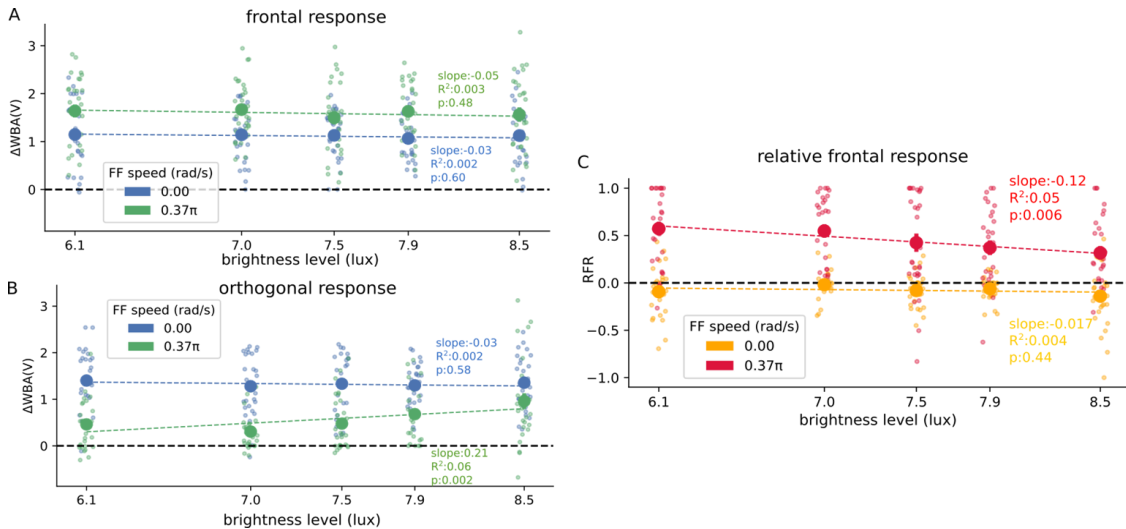
Figure 4. Results from experiments testing effects of varying levels of brightness on RFR with and without FF. (A) Steering responses to the frontally located annulus. (B) Responses to the orthogonally located annulus. (C) RFR for flies calculated from their frontal and orthogonal responses.

The first brightness experiment tested the effects of changing brightness during moving and non-moving FF condition on regional responsiveness. We used linear regression analysis to show the trends in orthogonal responsiveness, frontal responsiveness and the resulting RFR (Figure 4). We found a significant positive correlation between brightness and orthogonal responsiveness only in the moving FF condition (α=0.05) (Figure 4B). This brightness increase was not accompanied by a significant change in responsiveness in the frontal region for either FF case (Figure 4A). We also found significant negative correlation between the RFR and brightness in the moving FF condition which was not present in the non-moving FF condition (Figure 4C). These data support our hypothesis that attention shifts frontally in dim conditions, only

when that frontal region is predictably slower than orthogonal regions. Under non-moving conditions, frontal regions are not slower, so we predicted no forward-shifted attention. Though the data shows significant trends, the low R^2 values suggest that the model poorly accounts for attention shifts. Other factors likely influence their attention in this circumstance.

3.3 Flies rely more heavily on the frontal region when flying fast in low contrast environments
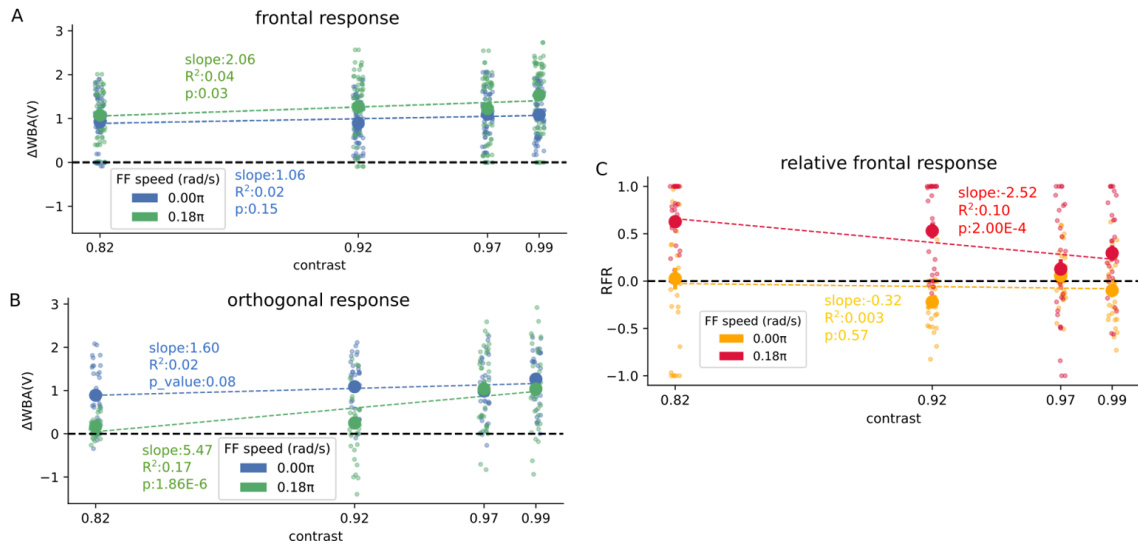
Figure 5. Results from experiments testing effects of varying contrasts on RFR with and without FF. (A) Steering responses to the frontally located annulus. (B) Responses to the orthogonally located annulus. (C) RFR for flies calculated from their frontal and orthogonal responses.

In our first contrast experiment we measured frontal, orthogonal and relative frontal responses under moving and non-moving FF conditions and four contrasts (Figure 5). We again used linear regression to identify response trends. We found significant positive trends in the orthogonal and frontal responses (Figure 5A and 5B) in the moving FF condition, not found in the non-moving FF conditions. RFR showed a significant negative trend as contrast increased in the moving FF condition (Figure 5C) suggesting that although the orthogonal and frontal regions

increased responsiveness under higher contrast conditions, the orthogonal region increased by more. As in the results of the previous brightness experiment, the R^2 was very low and therefore these models do not predict specific responses given contrast and FF. Other factors are likely to influence their responses.
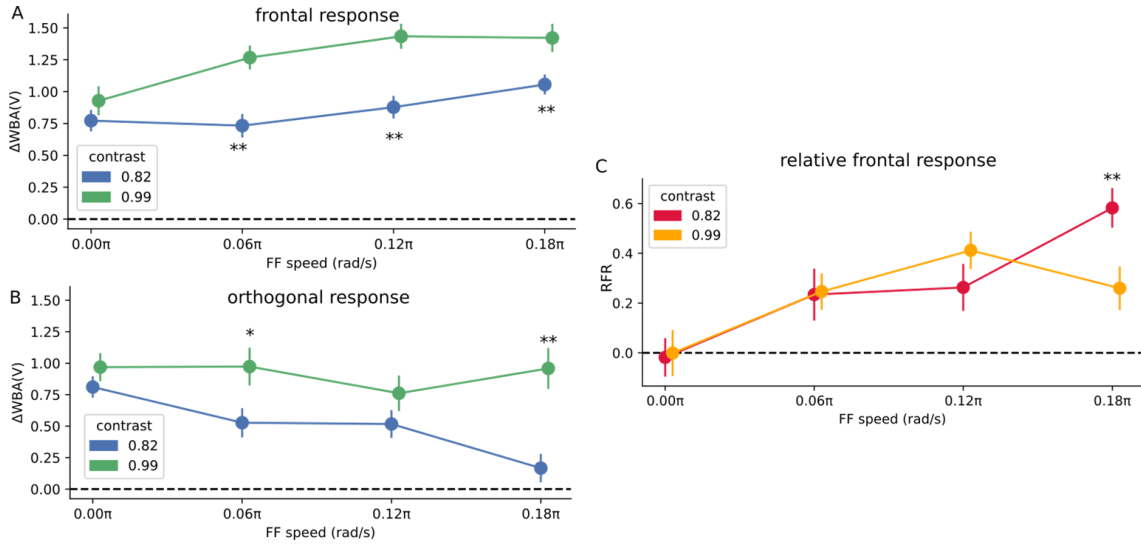
Figure 6. Results from experiments testing effects of varying FF speeds on RFR at high and low contrasts. Significant results from paired t-test shown with asterisk. (* p<0.05, ** p<0.005) (A) Steering responses to the frontally located annulus. (B) Responses to the orthogonally located annulus. (C) RFR for flies calculated from their frontal and orthogonal responses.

In the second contrast experiment we tested the highest and lowest contrast values of our previous experiment at four increasing FF speeds. Because previous research has already identified the positive trends between FF speed and frontal attention (Palermo & Theobald, 2019), our aim in this experiment was to determine significant differences between two contrast conditions at each FF speed (Figure 6). We found that in general, responses were significantly greater in the high contrast condition for both orthogonal and frontal responses under moving FF conditions (Figure 6A and 6B). The RFR was significantly greater in the low-contrast condition at the fastest FF speed (Figure 6C). Therefore, the results suggest that, although all steering responses tend to diminish with

decreased contrast under moving FF conditions, the RFR remains relatively unchanged until the fly experiences faster FF conditions. Under those faster low-contrast conditions, the fly relies proportionally greater on its frontal visual field for steering.

4. Discussion

Our simulation demonstrates why shifting attention to the frontal visual field is a viable strategy for flying animals. H was reduced in the orthogonal visual regions of the forward moving fly and low contrasts and brightnessess both reduced H even further. In the stationary condition, H decreased equally throughout the entire visual field so shifting attention forward would not provide any benefit.

The results from our experiments agree with the model and show that fruit flies assess brightness and contrast of scenes to determine where to focus their attention during flight. Flies actively shift attention from faster orthogonal visual regions to slower frontal regions to compensate for losses in the contrast and brightness of visual scenes. Flies can use this strategy to avoid relying on noisy parts of wide-field motion signals. If attention shifts reduce the area of the visual field used by flies, it may explain why flies don't always rely on the frontal visual field. Reducing the visual field might be problematic for attention-shifted flies since wide field motion signals become more ambiguous in narrow fields of view (Krapp et al., 1998). Alternatively, flies might instead weight the frontal visual field more heavily during attention shifts without changing the overall area of the visual field they navigate with. If flies use this method, then another potential reason flies might be conservative with attention shifting is that, although they can reduce the image noise by relying on slower-moving objects near the visual point of expansion, those

objects are likely to be further away, and therefore provide weak translatory steering cues.

The reductions in orthogonal response are dramatic over the small brightness and contrast ranges that we have tested here. Our experimental setup limited us to dim light levels, limiting the range of intensities we tested in this experiment. It is possible that in brighter conditions, small variations in brightness and contrast, like those tested here, lead to insignificant reductions in H. Brighter conditions might show much more gradual shifts of attention over a larger range of light intensities and contrasts.

Future work on the attention-shifting strategy will focus on modeling regional H of the insect eye as it translates or rotates in arbitrary directions through environments that can vary in qualities such as clutter, brightness, contrast, and depth. Though we've shown here that H is important for determining where a fly will attend to, the importance of other types of information besides spatial information should be investigated. Developing protocols to test these models in free-flying insects will help verify their results.

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CHAPTER IV
FLYING FRUIT FLIES MAINTAIN THE OVERALL ATTENDED AREA OF THEIR
VISUAL FIELD DURING ATTENTION SHIFTS
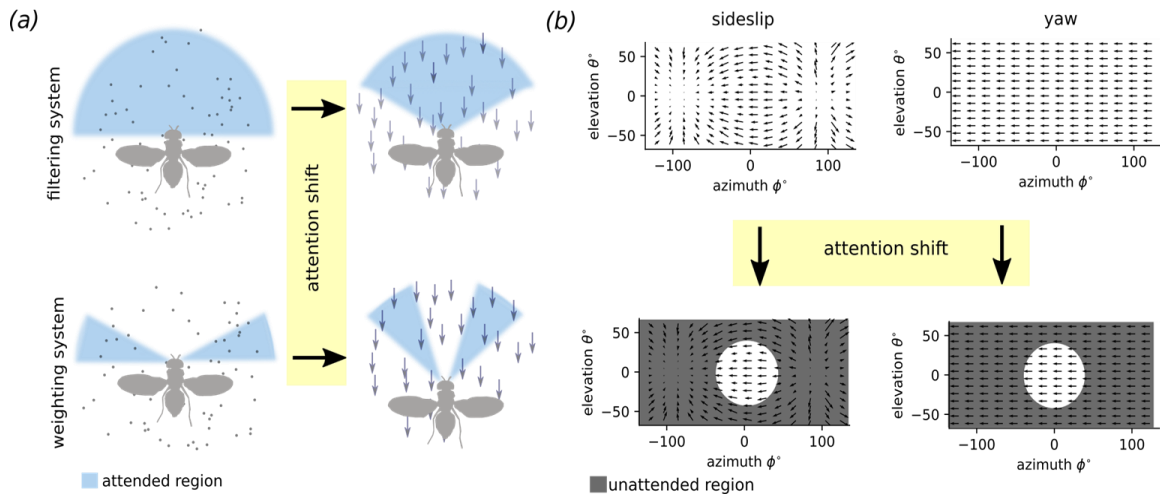
Figure 1. (a) Two possible methods to shift attention. Only the frontal half of the visual field is considered. The left column shows a slow-moving fly before shifting its attention. The right column shows the fly's shift in attention after its forward flight speed increases. In the top row, a filtering system is shown in which the attention shift results in an overall reduction of the area of the attended region. The bottom row demonstrates a weighting system for the attention shift which maintains the overall area of the attended regions (b) This figure has been modified from Krapp et al. (1998). Demonstration showing how attention shifts that result in reduced visual area can lead to perceived ambiguities in optic flow fields. Only the frontal portion of the visual area from ϕ = -110º to +110º and θ = -70º to +70º is shown. Top column shows the translational sideslip and rotational yaw optic flow perceived by a non attention-shifted fly. The bottom row shows the remaining portion of the attended region after the fly shifts its attention forward. The perceived optic flow fields in the attended regions after the shift are more ambiguous than those perceived before the shift.

1. Introduction

In dim environments visual signals become noisy. The statistical variance in photons arriving at light detectors from an image source is relatively high which makes it difficult to extract meaningful information from the signal. This results in a low signal-to-noise ratio (SNR). Fast-moving light detectors also experience low SNRs because few photons arrive at the detectors after they leave the image source. With large light-capturing apertures, visual systems can overcome the challenge of processing these otherwise noisy signals, although this is not a viable solution for small flying animals due to inherent restrictions in their size.

Despite these size limitations, flying insects rely heavily on vision to detect perturbations from their flight paths and correct for unintended motion. During flight, insects use optic flow fields to assess their self-motion (Borst & Haag, 2002; Götz, 1968). Optic flow fields are presented as two-dimensional vector maps which show the local image velocity of points over the visual field (Koenderink & Doorn, 1987; Nakayama & Loomis, 1974). These fields have predictable patterns during translational and rotational motion which makes them ideal for insects needing fast and accurate assessments of self-motion (Holger G. Krapp & Hengstenberg, 1996).

Fruit flies (*Drosophila melanogaster)* have characteristic flight patterns consisting of predominantly forward bouts, punctuated by brief turning saccades (Collett & Land, 1975; Hateren & Schilstra, 1999; Muijres et al., 2015; Tammero & Dickinson, 2002). Therefore, the majority of flight time a fruit fly is experiencing forward optic flow with occasional brief but imperceptibly fast yaw flow fields. Optic flow fields resulting from translational motion, including forward optic flow, have image speeds that vary considerably throughout the field. During forward optic flow, image speeds of elements in front are slow but increase as they pass by the side, resulting in significant reductions in SNR in orthogonal regions.

To compensate for lost SNR, fast forward flying fruit flies shift attention away from orthogonal regions and instead increase reliance on the slower-moving frontal parts of the flow field (Palermo & Theobald, 2019). To perform these shifts, flies determine forward speed and adjust attention accordingly. But if forward flow fields are always faster in the orthogonal region, why do flies not simply maintain attention in the front?

The cost of maintaining the neural feedback system required to shift attention might be offset by some benefit provided by the orthogonal portions of the flow fields.

The answer to this question depends on the overall shape of attention shifts. When an attention shift occurs, it can take one of two possible forms depending on whether the area of the attended field of view changes as the shift occurs. In one form, the fly uses a weighting system to assess SNR across regions of the eye and shift attention to less noisy areas without decreasing the overall attended visual area. In another form, the fly uses a filtering system to remove the noisy orthogonal portions, effectively narrowing the field of view (figure 1*a*). Which form the attention shift takes is unclear from previous methods(Palermo & Theobald, 2019) because the lack of response to a steering stimulus may be caused by filtering during the attention shift, or it may be caused by the fly anchoring to the non-steering portions of the stimulus as these regions become more weighted. Testing for some of the secondary consequences of these shifts may provide more substantial information about their form.

To perceive wide-field motion, fruit flies need to sample motion from local detectors over the entire eye (Borst & Egelhaaf, 1989; Werner Reichardt, 1987). In the fly brain, the lobula plate tangential cells (LPTCs) are large interneurons responsible for detecting wide-field motion by pooling together responses from the retinotopically organized one-to-one responses arriving from upstream ommatidia (Borst & Haag, 2002). During attention shifts, fruit flies modulate the signals from local regional motion detectors somewhere along this pathway.

The wide receptive fields of LPCTs, which span about 120 degrees, help prevent ambiguous perceptions of self-motion (Gauck & Borst, 1999; H. G Krapp et al., 1998).

These ambiguities arise when flies rely on only small portions of optic flow fields because two different types of self-motion appear nearly identical through narrow fields of view (Figure 1B) (Holger G. Krapp & Hengstenberg, 1996). Therefore, if fruit flies use the filtering method to shift attention, then they are relying on a smaller area of the flow field. Steering responses to narrow fields of view would differ depending on what the visual system interprets the motion to be, a phenomenon called multistable perception which has been found in fruit flies (Sterzer et al., 2009; Toepfer et al., 2018). Therefore, one reason fruit flies using this method would reserve attention shifting only during fast forward flight would be to reduce the likelihood of errors from ambiguous small-field motion signals. We tested this hypothesis in the virtual arena by determining whether tethered *Drosophila melanogaster* increase steering errors when attention-shifted and whether these errors are due to deficits in accuracy, precision or both. We then compared steering errors with those of tethered flies forced to steer with narrow fields of view to see if the narrowing of the attended visual field explained increased steering errors.
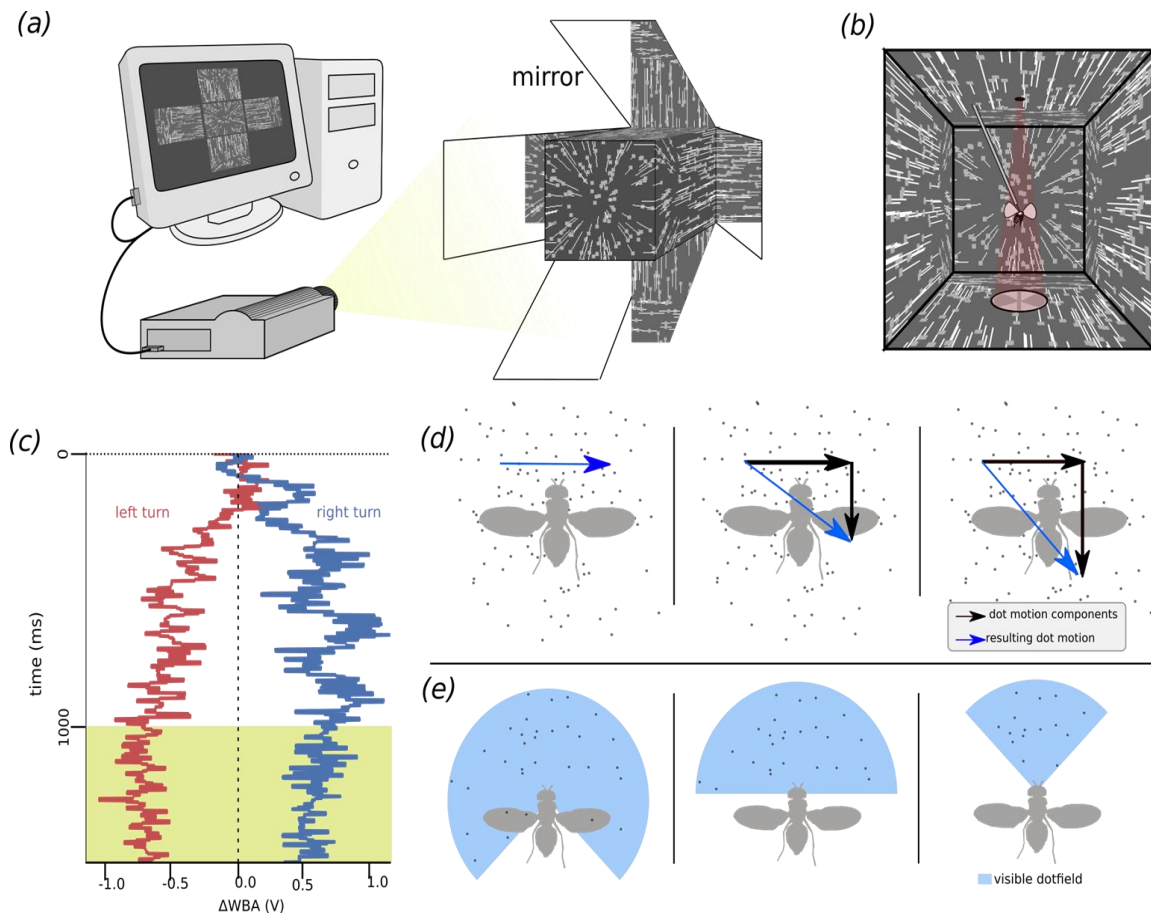
Figure 2. (a) A computer controls the stimuli that are projected onto the front face and side walls of the virtual flight arena via mirrors. (b) The fruit fly is tethered to the center of the inside of the arena cube. An infrared beam is shone onto the dorsal region of the fly and the wingbeat shadows are recorded by a pair of infrared detectors below the fly. (c) Sample left minus right wingbeat amplitude (ΔWBA) data collected from one fly during two separate trials. The negative ΔWBA values indicate an attempted left turn during one trial and positive values indicate an attempted right turn in another trial. The yellow region shows the last 400ms of the trials which were used for analysis. (d) Demonstration of how the forward speed conditions were generated in the first experiment. Only 3 examples of the 8 forward speeds are shown. The blue arrow indicates the actual motion of the dots during the trial, while the black arrows indicate the lateral and forward components of the dot motion. Only the forward component of the motion was changed between all the forward speed conditions. (e) Examples of the conditions used in the second experiment. The top-down cross section of the spherical cap which demarcates the visible dot field area is shown. This visible area was changed by adjusting the angle of the spherical cap's edge measured from the fly. The relative size of the spherical cap volume and the fly are not drawn to scale.

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2. Methods

2.1 Virtual flight arena

The virtual flight arena was a cube constructed from acrylic sheets with edges 200mm long. In order for researchers to have access to the cube, the rear face was removed. A modified DepthQ, WXGA-360 projector displayed images simultaneously onto the remaining 5 faces of the cube by a series of angled mirrors (figure 2*a*). The cube faces were lined with back-projection material so that the images displayed on the outside of the cube are visible to a fly inside.

2.2 Subjects and preparation

We reared female *Drosophila melanogaster* on a standard food medium under a 16h:8h light:dark cycle. The flies were collected and tested 4-6 days after eclosion. Flies were cold-anesthetized and tethered to a 0.1mm diameter tungsten rod attached to their mesonotum. They recovered at room temperature for 30 minutes. We suspended them in the center of the arena by their tether for testing. We dimmed the lights in the room during preparation for at least 15 minutes and for the duration of testing. Flies in each experiment performed all trials only once.

2.3 Steering responses and data collection

To measure responses to visual stimuli, we shone an infrared light onto the dorsal side of the fly as it was tethered in the center of the arena. Flapping wings cast shadows onto a photodiode below (figure 2*b*). A wingbeat analyzer measured the current from the photodiodes to extract the amplitudes of wingbeats and report them as voltages to the data acquisition computer. Flies adjust the difference between their right and left

wingbeat amplitudes during corrective steering responses (Götz, 1968). Steering was therefore recorded as the difference between the left and right wingbeat amplitudes, ΔWBA (figure 2*c*). For all trials, only the last 400 ms was used to calculate ΔWBA, as responses stabilized at this time. Each condition in each experiment was presented once with leftward motion, and again with rightward motion. The ΔWBA for each pair was averaged after sign correcting the response so positive values indicated steering in the direction of the cue.

2.4 Visual stimuli

We conducted two separate experiments consisting of multiple 1.2 second trials with 2.5 second rest periods between trials. During rest periods, flies controlled the angular position of a vertical white bar. Flies tend to fixate vertical bars in front and the ability to do so was the only inclusion criteria we used for trials (Heisenberg & Wolf, 1979; W Reichardt & Wenking, 1969). We did not analyze wingbeat readings collected during rest periods. The stimuli used in every experiment were virtual three-dimensional dot fields in a uniform random distribution surrounding the fly (density of 17 dots/steradian). Dot density remained constant across all conditions regardless of whether portions of the field were masked by the stimulus.

In both experiments, translating dots were perspective-corrected so closer dots had a higher angular speed than those further away. As a result, dots provided parallax as well as velocity information. We report dot speeds as the maximal mean speed passing the fly. Because dots did not rotate, the maximal mean speeds occurred orthogonal to the optic flow direction. For example, during forward optic flow, the maximal mean speeds

of the dot field were along the fly's transverse plane. The order of all conditions for each experiment was randomized to remove any order effects.

2.4.1 Stimuli to test the effects of forward optic flow speed on steering errors

To test the effects of forward attention shifting on steering errors we moved the dot fields front to back to simulate forward flight (FF) at 8 different speeds (0.00π, 0.05π, 0.11π, 0.16π, 0.21π, 0.26π, 0.32π, 0.37π radians/s). To create the steering stimuli for this experiment, each forward speed was compounded with lateral sideslip flow at 0.37π radians/s (figure 2*d*). The compounded motion started at the beginning of the trial and continued through its duration. Fruit flies make corrective steering responses in tethered flight when presented dot fields with lateral motion (Theobald et al., 2010). We tested 20 flies for this experiment.

2.4.2 Stimuli to test the effects of reduced visual area on steering errors

To test the effect of visual area on steering precision, we provided a steering stimulus of laterally moving dots while masking different regions of the visual field. Translation vectors during these sideslip disturbances were kept at the same magnitude as those in the previous experiment, but without the forward component of the motion. For each trial dot fields covered one of six possible fields of view (0.16π, 0.44π, 0.85π, 1.34π, 1.88π, 2.43π steradians). The visible portion of the dot field for each trial was contained within the dimensions of a spherical cap that started in front of the fly along the anterior-posterior axis and ended at an angle from forward (0.13π, 0.22π, 0.30π, 0.39π, 0.48π, 0.57π radians) (figure 2*e*). The remaining dot field was masked with a contrast-free region of average brightness equal to that of the visible portions of the field. We tested 36 flies for this experiment.

2.5 Analysis methods

For both experiments, we used a Shapiro-Wilk test to test for the normality of ΔWBA responses across all flies. To analyze the dispersion in responses of the group and of individual flies we first normalized the ΔWBA of each fly to the maximum of the mean response of all flies at each condition. Comparing unstandardized dispersion across different test conditions risks showing relatively larger dispersions for trials that simply had larger mean responses. Relative steering response deviations dictate the overall flight path deviation in free flight, and are therefore considered here. We used a linear regression analysis on the standard deviations of the ΔWBA responses among all flies to identify trends in the dispersion of the group mean responses with each changing condition. To analyze dispersion in fly responses over the time of each trial, we calculated the mean absolute deviation (MAD) of responses of each fly over the last 400ms of the trial.

3. Results
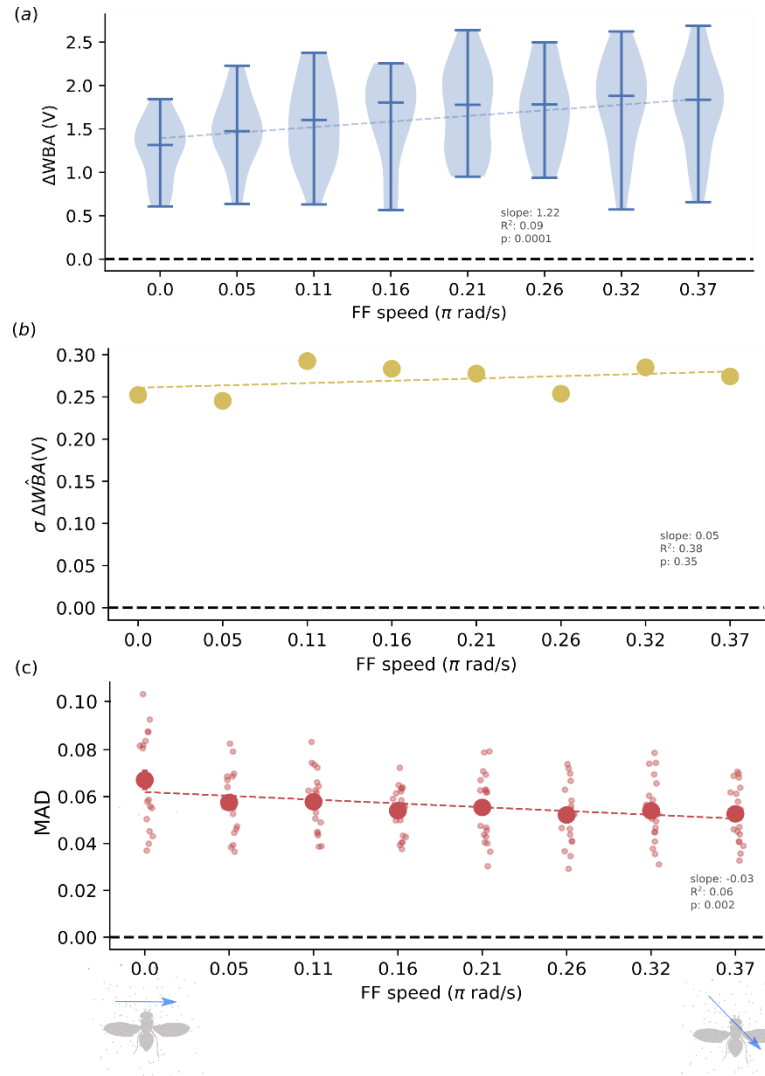
Figure 3. Results from the experiments testing the effects of FF speed on steering dispersion. (a) The mean steering responses of flies in the first experiment at each of the 8 forward optic flow speed conditions. (b) The standard deviation of the normalized ΔWBA responses across all flies in each condition. (c) The calculated MAD of each fly at each condition.

3.1 Flies do not lose steering accuracy or precision with increased forward flow speed

Flies increased ΔWBA as forward optic flow speed increased ($p = 0.001$, $r^2 = 0.09$) (Figure 3a). All responses at each forward optic flow speed were normally distributed ($p =$

0.95, 0.98, 0.96, 0.90, 0.95, 0.96, 0.96, 0.97, from slowest to fastest FF speed). We found

no significant trend in the standard deviations of the normalized responses across all
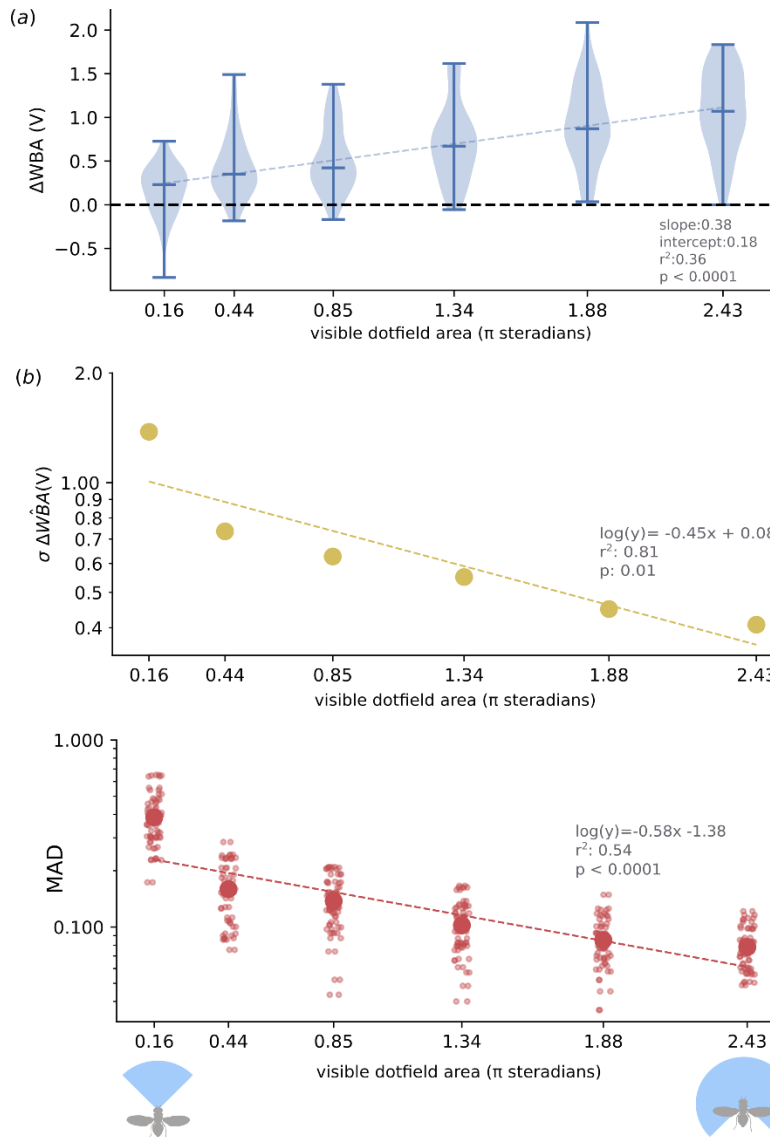
conditions (p=0.35)

(Figure 3b). We found a

significant downward

trend in MAD as the FF

speed increased (p=0.002,

r^2=0.06) (Figure 3c).

Figure 4. Results from the experiment testing the effects of reduced fields of view on steering response dispersion. (a) Violin plots show the median steering responses for flies at each visible dot field area condition. Regression analysis of mean responses are shown. (b) The standard deviation of the normalized mean steering responses for all flies at each visible area condition. (c) The calculated MAD for each fly at each visible area condition.

Eight outliers of the 160 data points were removed for the MAD analysis. Outliers were

defined as any data point more than three standard deviations from the mean.

3.2 Flies lose accuracy and precision when forced to navigate with a narrow field of view.

Flies increased mean responses as the visible dot field area increased ($p<0.0001$, $r^2=0.36$) (Figure 4a). The responses at each visible-area condition were normally distributed ($p= 0.40, 0.79, 0.65, 0.68, 0.83, 0.70$, from smallest to largest visual area). We also found a significant downward trend in the standard deviations of the normalized ΔWBA across all flies as the visible dot field area increases ($p=0.01$, $r^2=0.81$) (Figure 4b). There were significant downward trends in the MADs as the visible dot field area increased ($p<0.0001$, $r^2=054$) (Figure 4c). Eighteen outliers out of the 216 data points were removed for the MAD analysis.

4. Discussion

Fruit fly attention shifts in response to fast-forward optic flow sustain steering accuracy during tethered flight. We saw no increase in the dispersion of the mean responses of the group nor did we find increased dispersion in the responses over time. Our findings suggest that the attention shifts do not result in loss of accuracy or precision during tethered flight. The lack of increased errors indicates that flies may be using the weighting method for performing attention shifts. Instead, we found an opposite relationship where flies subjected to faster forward flight speeds had reduced MADs. This may be an artifact of forced forward optic flow presented to the fly which can cause some flies to perform avoidance turn-around responses (Reiser & Dickinson, 2013). As forward

flow increased, avoidance responses may remain the same but be biased towards one direction.

In contrast, tethered flies forced to navigate with narrow fields of view do increase steering errors as shown by the increase in dispersion of responses over time. We saw increases in both dispersion of mean responses of the group, and dispersion of responses over time. Therefore, we conclude flies lose accuracy and precision when forced to steer with narrow fields of view. The steering responses to narrow fields were normally distributed and do not indicate flies had multistable responses.

These results indicate that when flies are forced to steer with reduced visual fields, they make more errors. The absence of increased errors in the first experiment implies flies must instead shift attention without reducing the overall visual field. Based on these findings we believe flies are shift attention with a weighting method which allows them to retain steering accuracy even under fast conditions. This method ensures constancy in the overall amount of sensory information arriving to downstream neural integrators for efficient processing.

4.1. Conclusions

Flies are specially adapted to flying under challenging visual constraints. Here we show another example of the complex neural processing involved in stabilizing their flight. Attention-shifting is an active process by which flies relocate attention to regions of the visual field more likely to provide stronger signals for the inference of self-motion. How flies select regions to weigh during a shift requires further examination. Some regions are likely more informative for flight stability than others. For example, the

laterally positioned points of expansion and contraction during sideslip optic flow are

highly specific to this type of motion and would be a very informative cue. As a result, it

might be disadvantageous for a fly to shift attention away from these regions, despite the

unclear image they provide. Similarly, high SNR regions may not be beneficial if they

present little information about changes in trajectory. For example, a mountain on the

horizon may provide a clear image during fast flight but be too distant to provide

information about a translational disturbances. The information content of visual regions

must be considered against the clarity of the image they provide.

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CHAPTER V

CONCLUSIONS AND FUTURE DIRECTIONS

Flight control is a computationally demanding task. The impressive flying abilities of insects have captivated researchers and engineers developing flight control systems (Taylor & Thomas, 2003; Sun & Xiong, 2005). If we learn how high-performance small-mass insect flight control systems work, it potentially bolsters our development of unmanned automated flight vehicles. The field of psychology may also benefit from this information as it develops reductive models of sensory systems.

Our understanding of the sensory neurobiology that allows for insects to fly has greatly improved over the last 80 years. Throughout this research, the underlying challenge has always been to describe how something as small as the insect brain can process the necessary information to navigate, hunt, evade capture, forage, and perform other flight-related tasks. A large part of this challenge is figuring out what *necessary* means and what information is discarded.

Insects need to identify optic flow fields. The process of categorizing these flow fields into stereotypes allows flying insects to quickly respond to disturbances in self-motion (Krapp & Hengstenberg, 1996). But reducing all local motion signals arriving at the insect eye into a single self-motion category still provides challenges.

The visual world is complex with varied depth structure, clutter, and contrasts. Flight conditions are often unpredictable. Sensory systems which operate in these highly variable environments often depend on feedback loops so that they can sample the environment and adjust to increase operating efficiency. But maintaining a nervous system that performs these modifications is metabolically expensive, especially for tiny insects. For this reason, it was often assumed the insect visual system played a more

passive role in perceiving optic flow fields (M. Willis, personal correspondence, Jan 4, 2019).

Recent research has described some of the active processes involved in optic flow field perception. In dark environments, flying fruit flies perform directionally selective spatial and temporal neural pooling to effectively increase their sampling area and sampling duration of environmental light (Palavalli-Nettimi & Theobald, 2020). In this dissertation, I have presented attention-shifting as another active strategy in the fruit flies' repertoire. Attention-shifting allows the flies to reduce their reliance on the less informative portions of their visual field before they are integrated into the self-motion perceiving centers of the brain.

In chapter II, I described my initial observations of the attention shift process. As fruit flies navigate through their environment, the fast-moving objects in their peripheral vision suffer from motion blur. The low signal-to-noise ratio (SNR) in these blurry regions is a result of flies passing by scenes too quickly to detect sufficient photons from them. I found that in simulated fast flight, flies counteracted the effects of motion blur by instead steering with the frontal, slower portion of their visual field.

In chapter III, I described motion blur in terms of the loss of information capacity. I introduced the idea that scene brightness and contrast can also have similar effects to that of image speed on the quality of images that a region of the eye could render. Low contrast and dim environments worsen the already diminished SNR experienced by a fast-moving fly. I found that flies under these poor flight conditions will also shift their attention to the slower-moving frontal regions of their eyes because those regions have higher spatial information capacity.

In chapter IV, I tried to determine if flies resisted shifting attention forward due to loss of certainty about optic flow fields they were perceiving. Though it is impossible to test uncertainty directly, I used steering errors as a proxy. I found flies shift attention forward without any resulting increase in steering errors. But forcing them to steer with a reduced area field did result in higher steering errors implying that the attention shifts are not simply a removal of noisy visual regions, but weighting of different regions that maintains the overall effective visual area that they steer with.

These three chapters further our understanding of how attention-shifting contributes to the active processing of optic flow fields. The answers I found have only begun to describe the general principles that guide some of the attention-shifting behavior. Questions still need to be answered about the information content of visual regions when considering all the other types of self-motion beyond translational thrust and sideslip. There is likely inherent value in some regions because they are characteristic of certain types of flow. For example, rotational flow fields contain rotation points about the axis of rotation which are unambiguous. A goal of this work will be to build a model which given the structure of the environment, lighting conditions, and fly's self-motion, can predict where a fly attends to. Designing attention-testing protocols for free flight could also verify this model. Once verified, the model could be applied to autonomous vehicles to simplify the processing required for visually-guided navigation.

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