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Neural basis of target tracking in insects: Impact of body size and flight strategy

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THE CHANCELLOR, MASTER AND SCHOLARS OF THE UNIVERISTY OF CAMBRIDGE

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14. ABSTRACT

Motion vision can be broadly subdivided into two systems: one that codes for self-generated optic flow, and one that codes for objects that move independently of the remaining visual surround. Whereas the neuronal and behavioral algorithms underlying the detection of wide- field optic flow have been relatively well described, to the point where individual neurons of the input pathway can now be genetically silenced or activated (Borst, 2011), the mechanisms underlying target detection and pursuit are much less well understood. We have investigated this topic, and here summarize the proposed goals and the achievements (outputs in the form of manuscripts).
Goal 1 and 2: We have identified target sensitivity amongst descending neurons in killer flies, goggle flies (robber flies) and hoverflies. We have investigated through extracellular electrophysiology the responses to moving targets by descending neurons in these dipterans, to determine what information is extracted and how this information is encoded. Output: Nicholas S*, Supple J*, Leibbrandt R, Gonzalez-Bellido PT#, Nordstrm K#. 2018. Integration of Small- and Wide-Field Visual Features in Target-Selective Descending Neurons of both Predatory and Non-Predatory Dipterans. J. Neurosci. 50, 10725-10733...

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Neural basis of target tracking in insects: Impact of body size and flight strategy

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Contents

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1. Abstract

Motion vision can be broadly subdivided into two systems: one that codes for self-generated optic flow, and one that codes for objects that move *independently* of the remaining visual surround. Whereas the neuronal and behavioral algorithms underlying the detection of wide- field optic flow have been relatively well described, to the point where individual neurons of the input pathway can now be genetically silenced or activated (Borst, 2011), the mechanisms underlying target detection and pursuit are much less well understood. We have investigated this topic, and here summarize the proposed goals and the achievements (outputs in the form of manuscripts).

Goal 1 and 2: We have identified target sensitivity amongst descending neurons in killer flies, goggle flies (robber flies) and hoverflies. We have investigated through extracellular electrophysiology the responses to moving targets by descending neurons in these dipterans, to determine what information is extracted and how this information is encoded. Output:

Nicholas S*, Supple J*, Leibbrandt R, Gonzalez-Bellido PT#, Nordström K#. 2018. Integration of Small- and Wide-Field Visual Features in Target-Selective Descending Neurons of both Predatory and Non-Predatory Dipterans. J. Neurosci. 50, 10725-10733.

Nicholas, S, Leibbrandt, R, & Nordström, K (2019) “Visual motion sensitivity in descending neurons in the hoverfly” J Comp Physiol A Accepted

Goal 3: We have investigated the visual information that is behaviorally acquired prior to take-off, both in Hover flies and robber flies. We have determined the level of depth perception, and lack of therefore and prey size calculation before take-off in two species. Outputs

Thyselius M, Gonzalez-Bellido PT, Wardill T, Nordström K. 2018. Visual approach computation in feeding hoverflies. J. Exp. Biol. DOI: 10.1242/jeb.177162.

Fabian ST, Wardill TJ, Sumner M, Nordström K, Gonzalez-Bellido PT. Prey selection by the miniature robber fly Holcocephala fusca relies on estimation of absolute distance. (in preparation)

Goal 4: To describe the visual information that is behaviorally acquired during pursuit, and if optical adaptations play an important role in this calculation. Outputs:

Wardill TJ, Fabian ST, Pettigrew A, Stavenga DG, Nordström K. Gonzalez-Bellido PT. 2017. A Novel interception strategy in a miniature robber fly with extreme visual acuity. Curr Biol. 27, 854-859. (It was also the cover)

Dyakova, O, Mueller, M, Egelhaaf, M, and Nordström, K (2019) "Image statistics of the environment surrounding freely behaving hoverflies" J Comp Physiol A 205(3): 373-385

Wardill TJ, Knowles K, Barlow L, Tapia G, Nordström K, Olberg RM, Gonzalez-Bellido PT. 2015. The killer fly hunger games: target size and speed predict decision to pursuit. *Brain Behav Evol. Sep 24;86(1):28-37.*

Goal 5: To classify the attack strategies. We demonstrated that proportional navigation can predict the flight trajectories of both species, and did so by experimentally locating the appropriate delay and gain constant for each species. Outputs:

Fabian ST, Sumner ME, Wardill TJ, Rossoni S, Gonzalez-Bellido PT. 2018. Interception by two predatory fly species is explained by a proportional navigation feedback controller. J. R. Soc Interface 15: 20180466.

Additional Output: Review Articles and protocols

- *Dyakova, O* and *Nordström, K* (2017) "Image statistics and their processing in insect vision" **Curr Opin Insect Sci** 24: 7-14 doi.org/10.1016/j.cois.2017.08.002, IF 3.64

- Gonzalez-Bellido, PT, Fabian, ST, and *Nordström, K* (2016) "Target detection in insects: Optical, neural and behavioral optimizations" **Curr Opin Neurobiol** 41:122-128, IF 6.48\

- *Nicholas, S, Thyselius, M, Holden, M & Nordström, K (2018)* "Rearing and long term maintenance of *Eristalis tenax* hoverflies for research studies*"* **J Vis Exp,** 135: e57711, doi:10.3791/57711

2. Objectives

Under FA9550-15-1-0188 we have studied three distantly related fly species that we have chosen as they display extreme specializations for a similar behavior and differ dramatically in body size. The killer fly *Coenosia attenuata* has a body length of 3-4 mm; the goggle fly *Holcocephala fusca* is 5-7 mm long; and the hoverfly *Eristalis tenax* is 14-16 mm long. The target-pursuit behavior of killer flies and goggle flies is directed towards spotting and catching flying prey, whereas that of hoverflies is aimed at potential mates and/or territorial intruders, also on the wing. These three species therefore form an excellent cohort for a comparative approach that will inform us about the optimal behavioral and neural strategies for target tracking. Our main aim is to investigate whether *the difference in evolutionary history, biomechanics and size has obligated these three dipterans to develop different coding algorithms for target tracking, or are there similar underlying mechanisms, indicating the presence of a fundamental blueprint that provides the most efficient algorithm for target tracking?*

More specifically, our main objectives for the three years of study are:

(1) *To identify target sensitivity amongst descending neurons in killer flies, goggle flies and hoverflies.* We will use intracellular electrophysiology to investigate the responses to moving targets by descending neurons in the dipterans, to determine what information is extracted and how this information is encoded. We will reconstruct the neurons' anatomy to build a morphological atlas of the descending neurons.

(2) *To determine whether background motion and background clutter affect target visibility.* We will determine whether target responses of killer fly and hoverfly descending neurons remain robust in the presence of clutter and clarify if the type of background texture and of the specific optic flow components have an influence on the response to targets.

(3) *To describe the visual information that is behaviorally acquired prior to take-off.* We will determine the extent of depth perception and prey size calculation before take-off in the three species, by employing eye maps and 3D reconstructions of head movements, to calculate the experienced optic flow, and thus decipher if depth can be computed from the visual input.

(4) *To describe the visual information that is behaviorally acquired during pursuit.* We will identify at what point during the flight killer flies and hoverflies know that a target is the wrong size and abort the attack, and if background clutter and optical adaptations play an important role in this calculation. We will determine whether there is a sexual dimorphism in pursuit strategy.

(5) *To classify the attack strategies.* We will provide a mathematical description of the killer fly, hoverfly and goggle fly pursuits, and attempt to predict the trajectories based on parameters such as distance to prey, prey speed and direction, and provide a comparison to the strategies used by dragonflies.

3. Accomplishments/New findings

Goals 1 and 2:

To identify target sensitivity amongst descending neurons in killer flies, goggle flies and hoverflies.

To determine whether background motion and background clutter affect target visibility.

These goals have been met and published in the following manuscripts:

- **Nicholas S*, Supple J*, Leibbrandt R, Gonzalez-Bellido PT#, Nordström K#. 2018. Integration of Small- and Wide-Field Visual Features in Target-Selective Descending Neurons of both Predatory and Non-Predatory Dipterans. J. Neurosci. 50, 10725-10733.**

  [Journal Impact Factor: 5.97 Times Cited: 2]

- ***Nicholas, S, Leibbrandt, R, & Nordström, K* (2019) "Visual motion sensitivity in descending neurons in the hoverfly*"* J Comp Physiol A *Accepted***

We have successfully recorded descending neural activity in all three species, and corroborated the presence of Target Descending neurons in these flies.

In this publication, we have shown the interaction of the wide field system with the target tracking system, both normally carry visual information in parallel and simultaneously. However, at the premotor level, we found that activation of the widefield system suppresses the activity of the target tracking system.

Our findings are important because they demonstrate, for the first time, that although these animals are capable of detecting small and fast moving targets among clutter, the signal is suppressed by the optic flow circuit. This result is exciting because it demonstrates that either a) how the controller for proportional navigation is inbuilt into the system or b) that without the corollary discharge present during normal flight, the target tracking system is shut down, and thus optic flow requirements take priority.

Many additional recordings in killer flies and the robber fly Holcocephala fusca have been carried out. Thus, a second electrophysiology paper is in preparation.

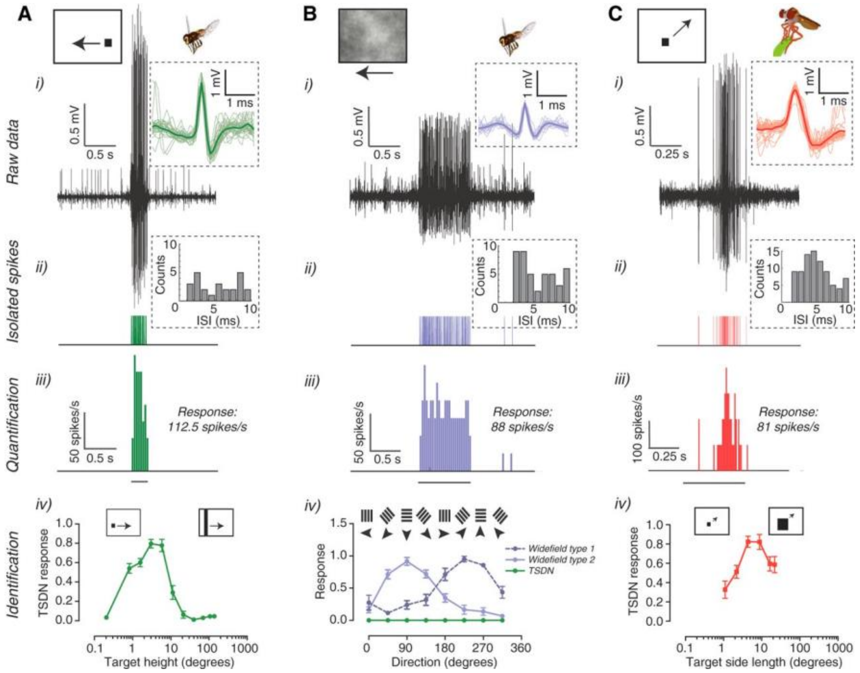


Figure 1 from Nicholas et a. 2018, demonstrating the presence of Target selective descending neurons in hover flies and robber flies.

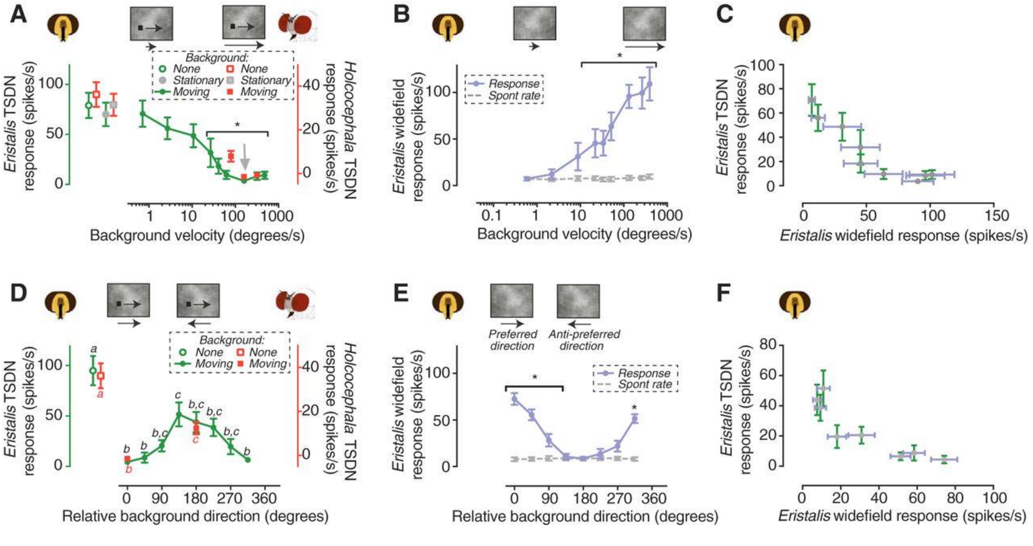


Figure 2 from Nicholas et a. 2018, demonstrating that simultaneous activation of the target tracking and optic flow systems results in suppression of the target tracking system

<u>Goal 3</u>:

To describe the visual information that is behaviorally acquired prior to take-off. We will determine the extent of depth perception and prey size calculation before take-off in the three species, By employing eye maps and 3D reconstructions of head movements, to calculate the experienced optic flow, and thus decipher if depth can be computed from the visual input.

<u>This goal was met by studying robber flies and hover flies. The hoverfly results have been published, and those from robber flies are written up and will be sent to review in the next few weeks:</u>

- **Thyselius M, Gonzalez-Bellido PT, Wardill T, Nordström K. 2018. Visual approach computation in feeding hoverflies. J. Exp. Biol. DOI: 10.1242/jeb.177162.**

[Journal Impact Factor: 3.32 Times Cited: 2]

This manuscript quantified the responses of feeding hover flies to incoming landing insect. It demonstrated that hover flies are cautious, taking off in response to most approaching objects, but doing so more quickly if the insect was a predator (wasp). Thus, this work contributes to our understanding of how fast flying insects take into account visual cues to make choices that can result in survival vs death.

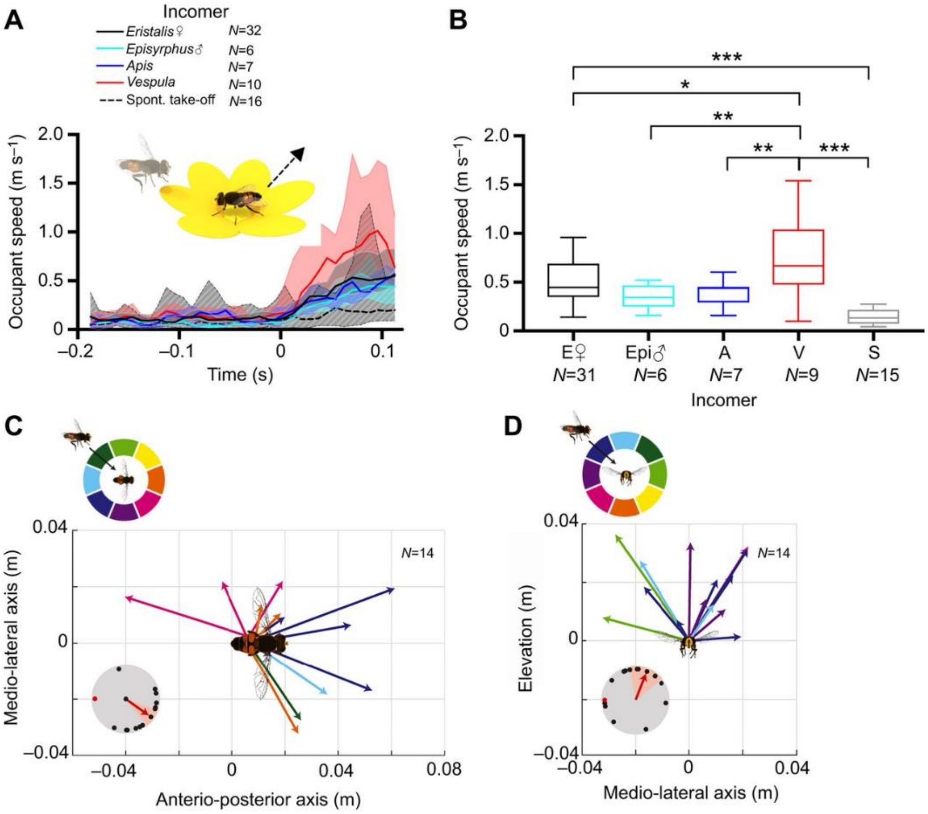


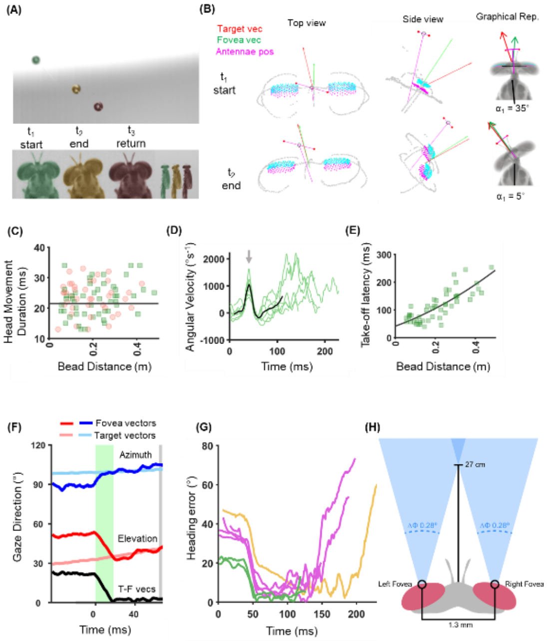
Figure 3 from Thyselius et al 2018. The occupant performs an escape response. (A) Occupant speed, color coded according to incomer identity (see key), as a function of the time of occupant take-off (at t=0). The dashed line shows the take-off speed when the occupant left the flower spontaneously. Thick lines show median, shadowing shows the interquartile range. The data have been smoothed using a third-order Butterworth filter with a cut-off frequency of 0.5. t=0 is the last frame before the occupant took off from the flower. We checked for outliers (Tukey) every 50 ms and excluded any insect that was classified as an outlier for a minimum of 4 time points. A two-way ANOVA with Tukey's multiple comparisons test from t=0 to 100 ms showed a time effect (P<0.001), species effect (P<0.001) and subject effect (P<0.001). (B) Box plot of occupant speed 50 ms after occupant take-off. E, Eristalis; Epi, Episyrphus balteatus; A, Apis mellifera; V, Vespula; S, spontaneous take-off. The midline is the median and error bars are after Tukey. Statistical significance was tested using one-way ANOVA followed by Tukey's multiple comparisons test: *P<0.05, **P<0.01, ***P<0.001. (C) The arrows show the positions of 14 occupants (female Eristalis) 100 ms after take-off, aligned to the position of the occupant at t=0, when viewed dorsally (as illustrated in the pictogram). The arrows are color coded to indicate the incomer approach angle (see color coding above graph). The inset shows occupant take-off angle (black dots) as a function of incomer position (red dot), where the red arrow indicates the mean (±s.e.m.) take-off angle. (D) The arrows show the positions of the same 14 occupants (female Eristalis) 100 ms after take-off, aligned to the position of the occupant at t=0, when viewed anteriorly (as illustrated in the pictogram). The arrows are color coded to indicate the incomer approach angle (see color coding above graph). The inset shows occupant take-off angle (black dots) as a function of incomer position (red dot), where the red arrow indicates the mean (±s.e.m.) take-off angle.

- ***Dyakova, O,*** **Mueller, M, Egelhaaf, M, and *<u>Nordström, K</u>* (2019) "Image statistics of the environment surrounding freely behaving hoverflies" J Comp Physiol A 205(3): 373-385**

- **Fabian ST, Wardill TJ, Sumner M, Nordström K, Gonzalez-Bellido PT. Prey selection by the miniature robber fly Holcocephala fusca relies on estimation of absolute distance. (in preparation)**

This paper is of importance because it will be the first to show that a small invertebrate predator uses absolute cues when assessing the suitability of flying targets.

Figure from Fabian et al. (In preparation) : Behavioral correlate of prey selection.



(A) Example images of *Holcocephala's* characteristic head movement to a passing target at three distinct time-points. These time-points include: t_1 when the head movement starts, t_2 when the head movement tracking the target ends, and t_3 when the head is returned to its resting position. (B) Gaze reconstruction of *Holcocephala* exemplified between times t_1 and t_2. (C) Head movement durations plotted against the distance to the target. Mean plotted by black line at 23 ms (n = 89). (D) Angular velocity of reconstructed head movements over time, where 0 is t1 (n = 7). Black line depicts a moving average. (E) Take-off latency of the flies after initial head movement (t1), plotted against bead distance at t1. Black line represents absolute error between fovea direction and target. (F) Example gaze direction during a head movement. Green shaded region represents high-velocity head-flick (t1 – t3). (G) The angle between gaze direction and bead vector to the target (termed heading error) over time. Colors highlight initial heading error with yellow being the greatest, pink the middling, and green the lowest. (H) Diagrammatic representation of the theoretical stereopsis limit (27 cm) of *Holcocephala* based on the convergence point of two parallel ommatidia, with interommatidial angles (∆ϕ) of 0.28°, separated by 1.3 mm (refer to paper where these measurements come from). Beyond 27 cm the fields of view overlap, reducing or nullifying the disparity in signal between the two ommatidia.

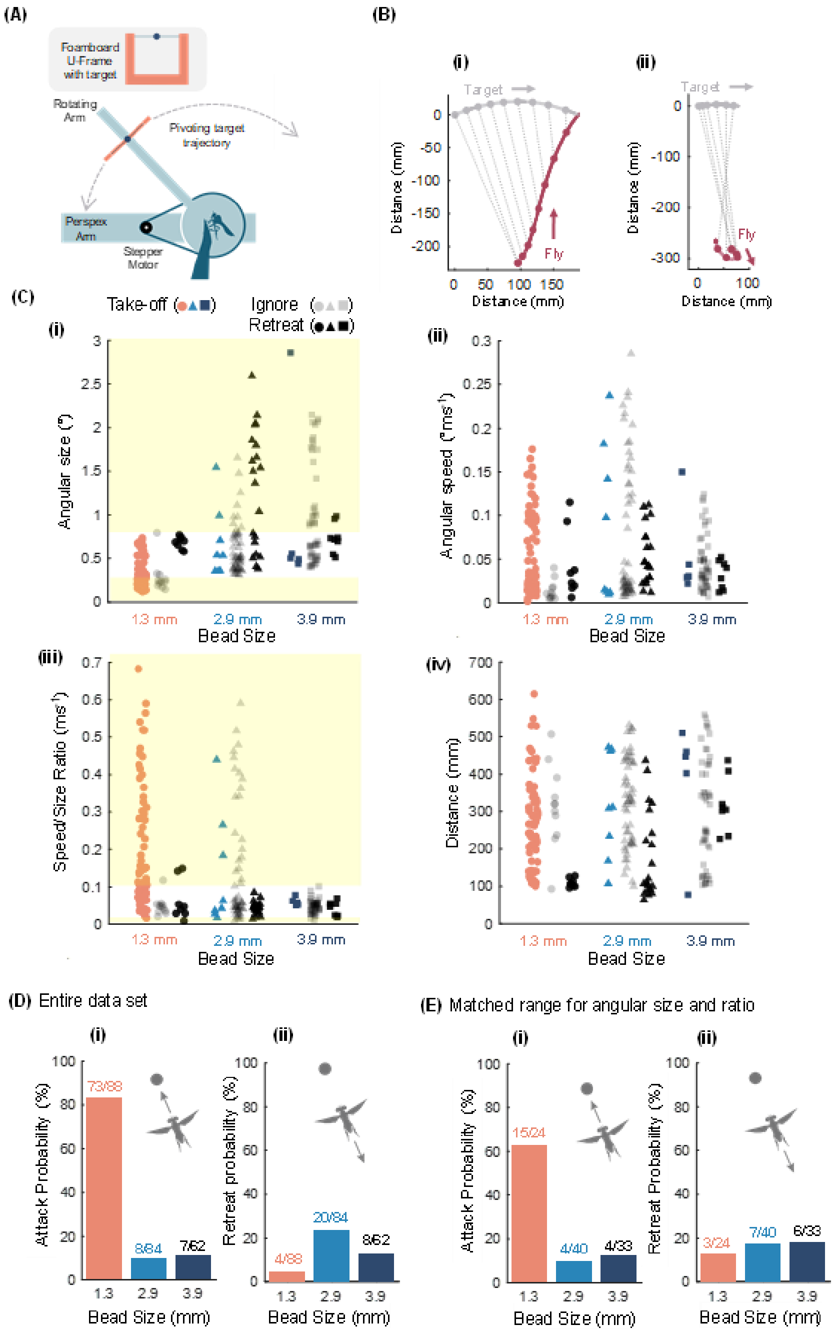


Figure from Fabian et al. (in preparation). Testing the use of absolute visual cues for target selection (A) Presentation of targets travelling in arcing trajectories. Individual targets are suspended on a foamboard U-frame, affixed to a rotating Perspex arm that is in turn driven by a stepper motor. (B) Example trajectories of *Holcocephala* (red) (i) intercepting and (ii) retreating from an arcing target (gray). Lines-of-sight (gray, dotted) are drawn at 50 ms intervals. (C) Actual target sized plotted against properties of presented arcing targets, split by fly response (color coding here). Properties include (i) angular size, (ii) angular speed, (iii) angular speed/size ratio, and (iv) distance. White region represents those targets used for closer analysis of an angular size and speed/size ratio matched dataset. (D) Response probabilities for the entire data set for both (i) attack responses and (ii) retreat responses. (E) Response probabilities for the matched angular size and speed/size ratio data set for both (i) attack responses and (ii) retreat responses

Goal 4: *To describe the visual information that is behaviorally acquired during pursuit.* We will identify at what point during the flight killer flies and hoverflies know that a target is the wrong size and abort the attack, and if background clutter and optical adaptations play an important role in this calculation. We will determine whether there is a sexual dimorphism in pursuit strategy.

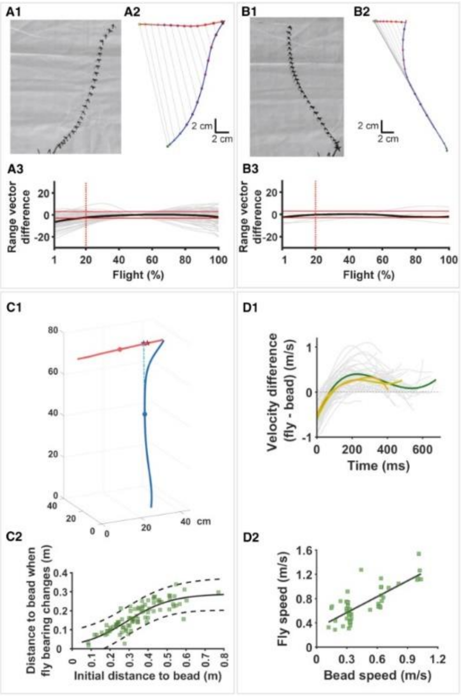
This goal was met, and the results published in two manuscripts:

- **Wardill TJ, Fabian ST, Pettigrew A, Stavenga DG, Nordström K. Gonzalez-Bellido PT. 2017. A Novel interception strategy in a miniature robber fly with extreme visual acuity. *Curr Biol*. 27, 854-859.**

[Journal Impact Factor: 9.25 Times Cited: 22]

This manuscript demonstrates how the eye of a miniature fly can reach the sensory performance of the largest dragonflies. In doing so, it challenged the dogma that small insects cannot develop predation strategies at the same level due to their sensory limitations. Within this work, we demonstrate that the flight trajectory is consistent with parallel navigation, and that the predator purposely slows down once it is within 30 cm, of the target. The navigation system then turns the fly backwards (a necessary action to keep parallel navigation), which results in much lower relative velocities between prey and predator, and thus higher probability of contacting the prey. This article was featured by NYTimes, National Geographic, BBC…etc.]

Figure 2 from Wardill et al 2018: Geometry and Timing of the *Holcocephala* Aerial Attack



(A1) *Holcocephala* flight trajectory toward a target moving at constant speed. (A2) 3D reconstructed trajectory of the flight course (blue curve) showing nearly parallel range vectors of decreasing length (target trajectory: red curve). (A3) The difference in direction (in degrees) between any one range vector (the line joining predator and prey at each frame) and the median range vector for the trajectory plotted for all trials in which *Holcocephala* chased a target moving at constant speed (n = 63; solid red lines = −3° and +3°; dotted red line: 20% of flight time elapsed; see also Figure S1). (B1 and B2) Flight trajectory when the presented bead changes velocity and completely reverses direction, during which *Holcocephala* maneuvers to keep the range vector parallel (see also Movie S1). (B3) During bead reversal presentations, the difference between the range vectors and the median vector stays close to zero (n = 4). (C1) Trajectory that would have resulted in a head-on collision interception (cyan dashed line), but before the collision *Holcocephala* arched backward (blue line). (C2) Distance to target when the change in heading occurs (black line: four-parameter sigmoidal fit; adjusted $r^2 = 0.73$; 95% confidence bounds shown by broken lines; n = 86). (D1) The difference in velocity between fly and bead. After the initial phase, the flies stop accelerating and keep their speed at a value that is slightly higher than that of the bead; this behavior is independent of attack duration (average short, medium, and long trajectories shown in short orange, medium lime, and long green lines, respectively). (D2) Fly speed as a function of bead speed. The average velocity during the lock-on phase is correlated with that of the bead (adjusted $r^2 = 0.6$; for all D plots, n = 51).

- **Wardill TJ, Knowles K, Barlow L, Tapia G, Nordström K, Olberg RM, Gonzalez-Bellido PT. 2015. The killer fly hunger games: target size and speed predict decision to pursuit.** ***Brain Behav Evol. Sep 24;86(1):28-37.***

[Journal Impact Factor: 1.91 Times Cited: 14]

This manuscript demonstrates that killer flies use very simple heuristic rules in order to gate the attack. This is adaptive because killer flies need to respond to a fleeting prey extremely fast, and thus are primed for making false positive mistakes over false negative ones. The same principle has recently been shown to apply to libellulid dragonflies, and thus it may be a universal principle for those animals who track targets but do not have access a measure of absolute distance.

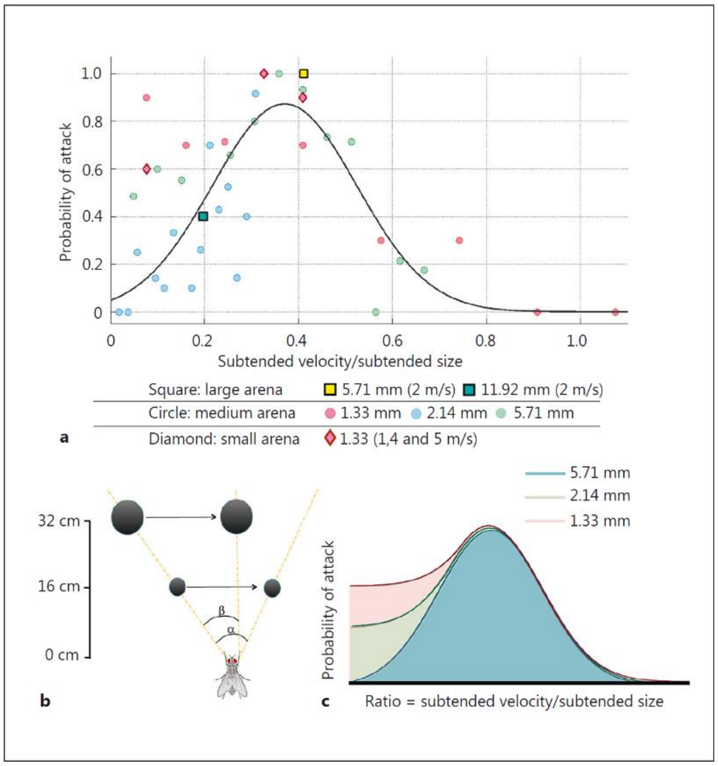


Fig. 3 from Wardill et al 2015. The probability of a killer fly attack is maximal when subtended prey velocity and size are proportional at a ratio = 0.37. **a** Plotting the probabilities shown in figure 2f against the ratio for each condition {ratio = [subtended velocity (°/ms)/subtended target size (°)]} aligns all data points and results in a Gaussian distribution with a peak at 0.37. Responses to the two largest beads (squares: 5.71 and 11.9 mm) tested in a larger arena follow the expected distributions. The 1.33-mm bead tested in a smaller arena also follows expected distribution at peak ratio. In addition, a high probability of attack is also seen at a ratio = 0.09 (red data). **b** The results highly suggest that killer flies can disambiguate large objects from suitable prey by linking the perceived velocity to the perceived size of the object. This is because a small object that is close will cover a wider retinal angle (α) than a large object that is far away (β) if both travel at the same velocity. **c** Stylized diagram of the results. Beads subtended a large size (5.71 mm presented at a 80-mm distance = 4.09°) will display a probability distribution explained by a Gaussian shape (blue area).Medium size beads (2.14 mm presented at a 80-mm distance = 1.53°) will display such Gaussian distribution and in addition have a tail at the lower ratios (green area). This probability tail becomes higher as the subtended size of the object decreases (1.33 mm, presented at a 80-mm distance = 0.95°, red area).

<u>Goal 5:</u> To classify the attack strategies. We will provide a mathematical description of the killer fly, hoverfly and goggle fly pursuits, and attempt to predict the trajectories based on parameters such as distance to prey, prey speed and direction, and provide a comparison to the strategies used by dragonflies.

<u>This goal was met, and the results published in the following manuscript:</u>

- **Fabian ST, Sumner ME, Wardill TJ, Rossoni S, Gonzalez-Bellido PT. 2018. Interception by two predatory fly species is explained by a proportional navigation feedback controller. J. R. Soc Interface 15: 20180466.**

[Journal Impact Factor: 3.35 Times Cited: 4]

This manuscript demonstrates that although the attack trajectories of two species of miniature flies look very different, they can be successfully modelled by a simple feedback mechanism called proportional navigation. Only the gain and latency of the system need to be tuned. Importantly, the tuned parameters fit with a 'best approach' for the ecologies of either fly.

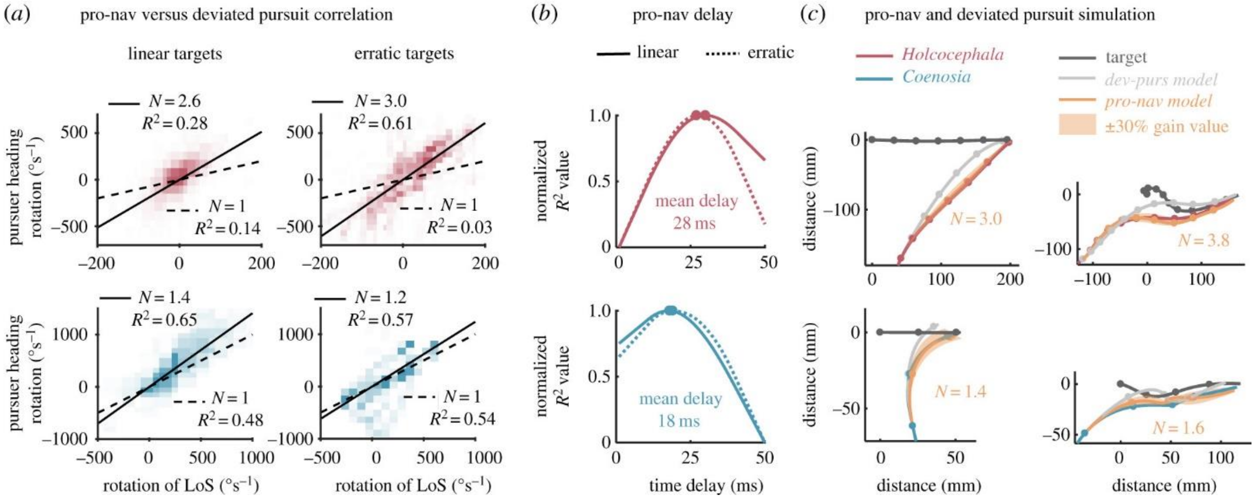


Figure 5 from Fabian et al. 2018. Fitting models for deviated pursuit and proportional navigation. (a) Purser heading rotation is plotted against the rotation of the LoS for both Holcocephala (red) and Coenosia (blue), shown for linear (left) and erratic (right) targets. Histograms of points are displayed with occupancy representing frequency count within a block. Data are displayed at the time delay that gave the highest coefficients of determination for a linear model. The best fitting pro-nav gain constant and resulting coefficient of determination are depicted top left each panel. Deviated pursuit (dev-purs) behaviour, where N = 1, is also tested for and the model gain and coefficient of determination displayed bottom-right of each panel. (b) Coefficients of determination, normalized from lowest to highest, are plotted against the respective applied time delay between stimulus and recorded response, with peaks marked by points. (c) Pro-nav flight simulations (compressed in two-dimensions) are plotted at individually fitted navigation constant values and best-fitting time delays, next to N = 1 dev-purs simulations, using flight speed and target position taken from recorded data. Points mark 50 ms intervals.

Additional achievements

In addition to meeting all the proposed goals with manuscripts, as described above, the following reviews and protocol manuscripts are also outcomes of this grant:

- *Nicholas, S, Thyselius, M, Holden, M &* *Nordström, K* (2018) "Rearing and long term maintenance of *Eristalis tenax* hoverflies for research studies*"* **J Vis Exp,** 135: e57711, doi:10.3791/57711
- *Dyakova, O* and *Nordström, K* (2017) "Image statistics and their processing in insect vision" **Curr Opin Insect Sci** 24: 7-14 doi.org/10.1016/j.cois.2017.08.002, IF 3.64
- Gonzalez-Bellido, PT, Fabian, ST, and *Nordström, K* (2016) "Target detection in insects: Optical, neural and behavioral optimizations" **Curr Opin Neurobiol** 41:122-128, IF 6.48\

4. Personnel supported

In Karin Nordström's lab, AFOSR funds supported Ph.D. students Olga Dyakova and Malin Thyselius. Dyakova performed the image analysis presented in this report, and Thyselius the behavioral work. In the lab of Paloma Gonzalez-Bellido, AFOSR funds supported Ph.D. student Sam Fabian and technician Mary Sumner. Sam defended his thesis in 2018, and it is now a postdoct in Imperial.

5. Complete List of Peer-Reviewed Publications Fully or Partially Supported by this Grant

Fabian ST, Wardill TJ, Sumner M, Nordström K, Gonzalez-Bellido PT. Prey selection by the miniature robber fly *Holcocephala fusca* relies on estimation of absolute distance. (in preparation)

Nicholas, S, Leibbrandt, R, & *Nordström, K* (2019) "Visual motion sensitivity in descending neurons in the hoverfly*"* **J Comp Physiol A** *Accepted*

Dyakova, O, Mueller, M, Egelhaaf, M, and *Nordström, K* (2019) "Image statistics of the environment surrounding freely behaving hoverflies" **J Comp Physiol A** 205(3): 373-385

Nicholas S*, Supple J*, Leibbrandt R, Gonzalez-Bellido PT#, Nordström K#. 2018. Integration of Small- and Wide-Field Visual Features in Target-Selective Descending Neurons of both Predatory and Non-Predatory Dipterans. ***J. Neurosci***. 50, 10725-10733.

Nicholas, S, Thyselius, M, Holden, M & Nordström, K (2018) "Rearing and long term maintenance of *Eristalis tenax* hoverflies for research studies*"* **J Vis Exp,** 135: e57711, doi:10.3791/57711

Fabian ST, Sumner ME, Wardill TJ, Rossoni S, Gonzalez-Bellido PT. 2018. Interception by two predatory fly species is explained by a proportional navigation feedback controller. ***J. R. Soc Interface*** 15: 20180466.

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6. Interactions

1. Participation/presentation at meetings, conferences, and seminars

Nordström is the Program co-chair of the 13th International Congress of Neuroethology, to be held in Brisbane, Australia, in July 2018.

Nordström and Gonzalez-Bellido co-organized a symposium (Neuronal mechanisms underlying target detection) at the 12th International Congress of Neuroethology, held in Montevideo, Uruguay in 2016.

Nordström organized a symposium (Vision in invertebrates: Decision making models, neural mechanisms, and quantitative behaviour) at the 36th Annual ANS Meeting, held in Hobart in 2016.

Nordström co-organized the Insect Vision: Cells, computation and behavior meeting, held at HHMI Janelia Research Campus, USA, in 2015.

Gonzalez-Bellido is a councilor for the Society of Neuroethology.

2. Presentations at International meetings by Gonzalez-Bellido.

2018 Quantitative Approaches to Naturalistic Behaviors. The Banbury Center of Cold Spring Harbor Laboratory (by invitation only, USA).

2017 SOAR Meeting (Oxford, UK).

2017 Neuroethology Gordon Conference (Lausanne, Switzerland).

2016 28th Cambridge Neuroscience Symposium (Invited Speaker, Cambridge, UK).

2015 "Moving the Senses: From Motion Sensing to Animals in Motion" (Bielefeld, Germany).