

An autonomous robot inspired by insect neurophysiology pursues moving features in natural environments

This content has been downloaded from IOPscience. Please scroll down to see the full text.

2017 J. Neural Eng. 14 046030

(<http://iopscience.iop.org/1741-2552/14/4/046030>)

[View the table of contents for this issue](#), or go to the [journal homepage](#) for more

Download details:

IP Address: 80.82.77.83

This content was downloaded on 18/07/2017 at 20:17

Please note that [terms and conditions apply](#).

You may also be interested in:

[Performance of an insect-inspired target tracker in natural conditions](#)

Zahra M Bagheri, Steven D Wiederman, Benjamin S Cazzolato et al.

[A small-scale hyperacute compound eye featuring active eye tremor: application to visual stabilization, target tracking, and short-range odometry](#)

Fabien Colonnier, Augustin Manecy, Raphaël Juston et al.

[Bio-inspired motion detection in an FPGA-based smart camera module](#)

T Köhler, F Röchter, J P Lindemann et al.

[Man-made velocity estimators based on insect vision](#)

Sreeja Rajesh, David O'Carroll and Derek Abbott

[Musca domestica inspired machine vision sensor with hyperacuity](#)

D T Riley, W M Harmann, S F Barrett et al.

[A analysis-based, controller-synthesis framework for robust bioinspired visual navigation in less-structured environments](#)

J Keshavan, G Gremillion, H Escobar-Alvarez et al.

[A biomimetic vision-based hovercraft accounts for bees' complex behaviour in various corridors](#)

Frédéric L Roubieu, Julien R Serres, Fabien Colonnier et al.



SCHOOL
FOR ADVANCED
STUDIES
LUCCA

2017/18 PhD program at
IMT School for Advanced Studies Lucca
Deadline for applications – July 31st 2017, 6 pm Italian time

An autonomous robot inspired by insect neurophysiology pursues moving features in natural environments

Zahra M Bagheri^{1,2}, Benjamin S Cazzolato², Steven Grainger²,
David C O'Carroll³ and Steven D Wiederman¹

¹ Adelaide Medical School, The University of Adelaide, Adelaide, SA, Australia

² School of Mechanical Engineering, The University of Adelaide, Adelaide, SA, Australia

³ Department of Biology, Lund University, Sölvegatan 35, S-22362 Lund, Sweden

E-mail: zahra.bagheri@adelaide.edu.au

Received 23 November 2016, revised 21 May 2017

Accepted for publication 6 June 2017

Published 13 July 2017



Abstract

Objective. Many computer vision and robotic applications require the implementation of robust and efficient target-tracking algorithms on a moving platform. However, deployment of a real-time system is challenging, even with the computational power of modern hardware.

Lightweight and low-powered flying insects, such as dragonflies, track prey or conspecifics within cluttered natural environments, illustrating an efficient biological solution to the target-tracking problem. **Approach.** We used our recent recordings from ‘small target motion detector’ neurons in the dragonfly brain to inspire the development of a closed-loop target detection and tracking algorithm. This model exploits *facilitation*, a slow build-up of response to targets which move along long, continuous trajectories, as seen in our electrophysiological data. To test performance in real-world conditions, we implemented this model on a robotic platform that uses active pursuit strategies based on insect behaviour. **Main results.** Our robot performs robustly in closed-loop pursuit of targets, despite a range of challenging conditions used in our experiments; low contrast targets, heavily cluttered environments and the presence of distractors. We show that the facilitation stage boosts responses to targets moving along continuous trajectories, improving contrast sensitivity and detection of small moving targets against textured backgrounds. Moreover, the temporal properties of facilitation play a useful role in handling vibration of the robotic platform. We also show that the adoption of feed-forward models which predict the sensory consequences of self-movement can significantly improve target detection during saccadic movements. **Significance.** Our results provide insight into the neuronal mechanisms that underlie biological target detection and selection (from a moving platform), as well as highlight the effectiveness of our bio-inspired algorithm in an artificial visual system.

Keywords: neurorobotic, target tracking, insect-inspired vision, insect neurophysiology

 Supplementary material for this article is available [online](#)

(Some figures may appear in colour only in the online journal)

1. Introduction

In recent years, there has been developing interest in the use of mobile robots for applications in industry, health and medical services, and entertainment products. Autonomous robots

gather information about their surrounding environment via sensors (e.g. optical, ultrasonic, or thermal sensors), process this information and initiate motor commands to complete specific tasks with a self-determined behaviour. Biological systems employ similar sensory-motor control and autonomy

to perform their daily activities. Thus, there is common ground in robotics and biology in understanding how such systems function and reverse engineering biological systems can provide blueprints for robotics applications.

Detecting and tracking a moving object against a cluttered background is among the most challenging tasks for both natural and artificial vision systems. Recent work has drawn inspiration from biological visual systems for the development of robust target tracking algorithms. For example, inspired by bird and fish behaviours, Zheng and Meng (2008) developed a population-based search algorithm, called particle swarm optimization and implemented it in an object tracking algorithm. Zhang *et al* (2010) proposed a model of target appearance for visual tracking that was inspired by the hierarchical models of object recognition in visual cortex (Riesenhuber and Poggio 1999). Mahadevan and Vasconcelos (2013) developed a bio-inspired tracker combining bottom-up centre-surround discriminations and a target-tuned top-down saliency detector. Inspired by the fly's visual micro-scanning movements, Colonnier *et al* (2015) developed a small-scale artificial compound eye, which estimates displacement by measuring angular positions of contrasting features. The researchers mounted the eye on a tethered robot and tracked contrasting objects (hands) moving over a textured background. More recently, Cai *et al* (2016) presented a biologically inspired target tracking model which partially mimics ventral stream processing in the primate brain.

These biologically inspired target tracking studies mainly focus on models of primate vision, however, insects provide an ideal group to draw inspiration from within the context of target tracking. Many species of flying insects, such as dragonflies, are capable of detecting, selecting and chasing tiny prey or conspecifics. This capacity is all the more humbling for robotics engineers considering the insects limited visual resolution ($\sim 0.5^\circ$) and relatively small size (brain less than 2 mm wide), light-weight and low-power neuronal architecture (Webb *et al* 2004). Remarkably, the dragonfly performs this task within a visually cluttered surround, in the presence of distractors (Corbet 1999, Wiederman and O'Carroll 2013a) and with a capture rate greater than 97% (Olberg *et al* 2000). Such performance motivates the design of an insect-inspired, visual target tracking algorithm for autonomous robot control.

Using intracellular, electrophysiological techniques to record neuronal activity within the insect optic lobe, our laboratory has identified and characterized a set of neurons we refer to as 'small target motion detectors' (STMD) that likely mediate target detection and pursuit. These neurons are tuned to the size and velocity of targets, are sensitive to their contrast, yet can respond robustly to targets even without relative motion between them and a cluttered background (O'Carroll 1993, Nordström *et al* 2006, Nordström and O'Carroll 2009, O'Carroll *et al* 2011, O'Carroll and Wiederman 2014, Wiederman and O'Carroll 2011). Inspired directly by these physiological data, we have developed a nonlinear 'elementary-STMD' (ESTMD) model for local target discrimination (Wiederman *et al* 2008) and have implemented this model in a closed-loop target tracking system using a virtual reality (VR) environment (Halupka *et al* 2011, Bagheri *et al*

2014a, 2014b, 2015b). We elaborated (Bagheri *et al* 2014a, 2015a) this closed-loop model to account for recent observations of 'facilitation' in STMD neurons (Dunbier *et al* 2011, 2012, Nordström *et al* 2011). Facilitation involves the spiking response of these neurons building over several hundred milliseconds as targets move along continuous trajectories and resets to their naive state when there are large spatial or temporal breaks in the trajectory (Dunbier *et al* 2011, 2012).

Using closed-loop simulations against cluttered natural scenes, we predicted that the optimum temporal properties of facilitation is dependent on the degree of background clutter and the purpose of the pursuit (i.e. predation or mating) (Bagheri *et al* 2015a). We also showed that **facilitation** not only improves pursuit success, it enhances the ability to 'attend' to one target in the presence of distractors (Bagheri *et al* 2015a). Simulations reveal robust performance, achieving high prey capture success rates even within complex backgrounds, for low contrast targets, or where the relative speed of pursued prey is high (Bagheri *et al* 2015a). We recently benchmarked our model against several state-of-the-art trackers and although less computationally expensive, it matched or outperformed them, particularly when tracking small moving targets in natural scenes (Bagheri *et al* 2015b, 2017).

Although our model is robust in simulation, the performance in response to uncertainties inherent within real environments (e.g. illumination changes, occlusions, and vibration) are as yet unknown. Moreover, robotic systems are limited by the sampling rate of their sensors, processing and actuators. It is unclear how our algorithm performs on a hardware platform, where inclusion of sensors and physical robot dynamics results in additional latency which may affect the stability of the feedback process.

In addition to engineering applications, bio-inspired robots can provide insight into the underlying, biological, sensorimotor system. For example, dragonflies must deal with turbulent air and vibration during the flight, whilst focusing on the target (Collett 1980, Krapp and Wicklein 2008). Furthermore, animals use eye or body movements to modulate the visual inputs (via closed-loop feedback) (Land 2015). An important question is how animal saccadic movement or environmental factors change neural responses underlying the detection and selection task. Our ability to investigate these questions in the biological system is limited, due to the open-loop nature of experiments (i.e. animal must be restrained). However, robots provide a suitable alternative to model such sensorimotor mechanisms all whilst embedded within real-world environments.

Here we present an implementation of our recently developed target-pursuit model on an autonomous, robot platform. We test the robot in both controlled conditions using an indoor environment projected with natural images, and in unstructured outdoor environments. We examine the effect of **environmental parameters**, **facilitation** and **saccadic movement** on robot performance. Our results show that even under demanding conditions (e.g. complex background clutter, illumination variation, presence of distractors, and vibration) our robotic implementation performs robustly with a success rate similar to that observed in simulations. Moreover, we identify

这些神经元对连续轨迹的响应

this 很重要 -> 增强模型

good outcome

可能未考虑的硬件计算问题

???

实验场景

研究变量

更深入的结论

several key principles for optimal performance of such a system under real-world conditions.

2. Methods

Figure 1 shows an overview of the hardware implementation of the insect-inspired tracker on a Husky A200 (Clearpath Robotics™) platform using ROS, C++ and OpenCV. A Blackfly camera (Point Grey Research Inc.) was mounted on the robot to capture video of the natural environment. Further details of hardware are provided in section 2.3. Camera output serves as input to the insect-inspired target tracking model which calculates target location. The pursuit algorithm uses target location to calculate a ‘saccadic’ turn (short and fast yaw turns to change direction of gaze) angle as seen in insect behaviour (Land and Collett 1974, Wehrhahn *et al* 1982, Mischiati *et al* 2015). The Matlab code for the insect-inspired target tracking model is downloadable via <https://figshare.com/s/377380f3def1ad7b9d44> (Bagheri *et al* 2017).

2.1. Insect-inspired target tracking model

The insect-inspired target tracking model is composed of three subsystems: (1) early visual processing (2) target matched filtering (ESTMD) (3) position selection and facilitation mechanism. Detailed model equations are presented in the Appendix.

2.1.1. Early visual processing. The optics of flying insects are limited by diffraction and other forms of optical interference within the facet lenses (Stavenga 2003). This optical blur was modelled with a Gaussian low-pass filter (full-width at half maximum of 1.4°), which is similar to the optical sampling of typical day-active insects (Stavenga 2003). The average inter-receptor angle ($\Delta\varphi$) between photoreceptors can vary from tens of degrees in Collembola to 0.24° in the acute zone of the dragonfly *Anax junius* (Land 1997). We sub-sampled the captured image at 1° intervals as an approximate match for the resolution of day-active flies (Straw *et al* 2006), balancing acuity with computational efficiency of the algorithm. The green spectral sensitivity of the motion pathway in flying insects was simulated by processing only the green channel of the RGB imagery (Srinivasan and Guy 1990). This pre-processing is considered as the ‘model input’ to the target tracking algorithm in further analyses.

Simulating biological vision (Srinivasan *et al* 1982), redundant information was removed with neuronal adaptation (temporal high pass filtering) and centre-surround antagonism (spatial high pass filtering). We simulated the temporal properties of photoreceptors and the 1st order interneurons, the large monopolar cells (LMCs), with a discrete log-normal function ($G(z)$) (Halupka *et al* 2011). The filter properties were matched to the temporal impulse response observed in LMC recordings (James 1990). Centre-surround antagonism as observed in physiological recordings was modelled by subtracting 10% of the centre pixel from the neighbouring pixels (H) which provides a zero DC spatial component.

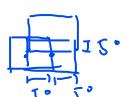
2.1.2. Target matched filtering (ESTMD stage). Rectifying transient cells (RTCs) within the insect 2nd optic neuropil (medulla) exhibit processing properties well suited as additional input processing stages for a small target motion detection pathway (Wiederman *et al* 2008). RTCs exhibit independent adaptation to light increment (ON channel) or decrement (OFF channel) (Jansonius and van Hateren 1991, Osorio 1991). The separation of the ON and OFF channel was modelled by half-wave rectification (HWR1). Each channel was processed through a fast adaptive mechanism, with the state of adaptation determined by a nonlinear filter that switches its time constant. Time constants were ‘fast’ ($\tau_{FA} = 3$ ms) when channel input is increasing and ‘slow’ ($\tau_{FA} = 70$ ms) when decreasing. This adaptation causes subtractive inhibition of the unaltered ‘pass-through’ signal. Additionally, we implemented strong spatial centre-surround antagonism, with each channel surround inhibits its next-nearest neighbours (see Wiederman *et al* (2008) for details). The temporal adaptation reduces responses to background texture, while strong surround antagonism conveys selectivity for local edge features (i.e. features that are small in the dimension orthogonal to the direction of travel). A second half-wave rectification (HWR2) was applied to the output of the strong centre- surround antagonism to eliminate the negative values (a thresholding nonlinearity observed in spiking responses).

In the direction of travel, small targets are characterized by an initial rise (or fall) in brightness, and after a short delay are followed by a corresponding fall (or rise). This property of small features was exploited by multiplying each contrast channel (ON or OFF) with a delayed version of the opposite channel (delayed using a low-pass filter ($LPESTMD$), $\tau_{ESTMD} = 25$ ms) and then summing the outputs. This also confers sensitivity to targets independent of the polarity of their contrast against the background.

2.1.3. Integration and facilitation. Neuron-like soft saturation of ESTMD outputs was modelled with a hyperbolic tangent function ($S(x) = \frac{1}{1 + e^{-x}}$), ensuring all signals lie between 0 and 1. The target location was calculated by implementing a simple competitive selection mechanism which chooses the maximum of the output values across the visual field. In the insect target-detecting system, there is a retinotopic array of small-field STMDs (SF-STMDs) which we hypothesise integrates local outputs of a number of underlying ESTMDs ($\sim 10^\circ \times 10^\circ$ region) (O’Carroll 1993, Barnett *et al* 2007).

A facilitation mechanism as seen in biological STMDs (Dunbier *et al* 2011, 2012, Nordström *et al* 2011) was implemented by building a weighted ‘map’ dependent on the location of the winning feature but shifted by a target velocity vector (an estimation of future target location). In the insect system, the visual information could be facilitated by a retinotopic array of SF-STMDs with overlapping receptive fields. We modelled the spatial extent of the weighted map by a grid of 2D Gaussian kernels (half-width at half maximum of 5°) with centres separated by 5° ($FG(r')$), providing a near optimum spatial size for the facilitation mechanism (Bagheri *et al* 2015a). This is equal to 50% overlap between

促进机制的建模文章



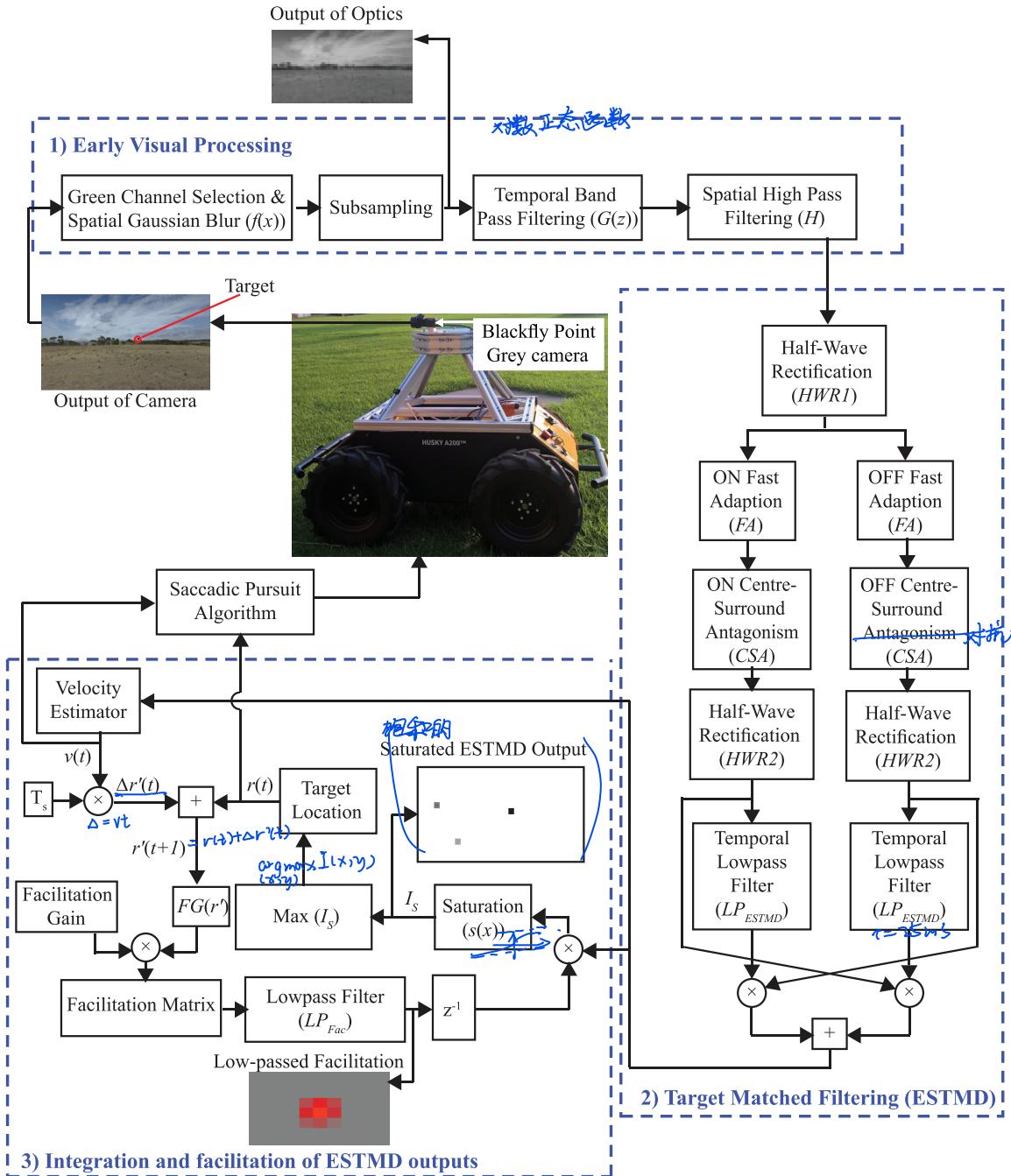


Figure 1. Overview of the hardware implementation of the insect-inspired tracking model. The robotic platform is a Clearpath Husky robot. A Point Grey Blackfly camera was mounted on the robot to capture input imagery. The camera output is processed by the insect-inspired, target-tracking model which calculates the target location. The insect-inspired target tracking model includes (1) early visual processing which mimics the response characteristics of optics, photoreceptors and large monopolar cells (LMC) in flying insects. (2) The ESTMD stage which includes rectification, fast adaptation and centre-surround antagonism provides a matched spatiotemporal filter tuned for small moving targets. (3) The recently observed ‘facilitation mechanism’ is modelled by building a weighted map (lowpass filter, time constant = τ_f) based on the predicted location of the target in the next sampling time ($r'(t + 1)$). The predicted target location was calculated by shifting the location of the winning feature ($r(t)$) with an estimation of the target velocity vector ($v(t)$) provided by the Hassenstein-Reichardt elementary motion detector which was multiplied with sampling time (T_s). The output of ESTMDs is multiplied with a low-pass version of a weighted map. The time constant of the facilitation low-pass filter controls the duration of the enhancement around the winning feature. The pursuit algorithm calculates the saccadic turn angle based on the detected target location and direction of target motion.

receptive fields of SF-STMD neurons. The ESTMD output was multiplied with a low-pass filtered (LP_{Fac}) version of this facilitation map. The facilitation time constant (τ_f) controls the duration of the enhancement around the location of

the winning feature. Four different time constants (varied in the range 40–2000 ms) spanning the typical facilitation time course (~200 ms) observed in dragonfly STMDs (Dunbier et al 2012) were tested in the experiments.

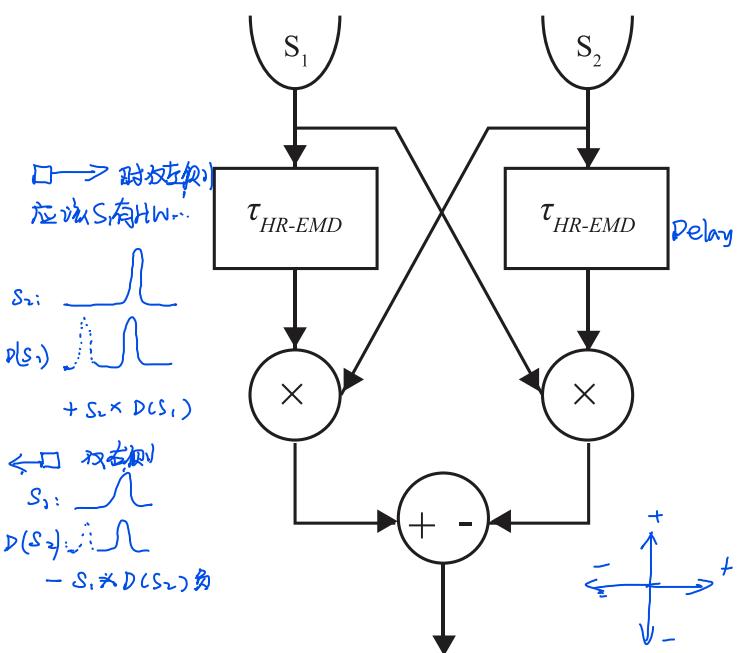


Figure 2. The Hassenstein–Reichardt elementary motion (HR-EMD) were used to estimate the velocity of the target. HR-EMD employs two spatially separated signals (S_1, S_2) and correlates them after a delay (via a low-pass filter, $\tau_{\text{HR-EMD}} = 40 \text{ ms}$) resulting in a direction selective output (Hassenstein and Reichardt 1956). Subtracting the two mirror-symmetric sub-units yields positive response for the preferred motion direction (in this case left to right) and a negative one in the opposite direction (right to left).

To provide an estimate for the future location of the target, we used the Hassenstein–Reichardt elementary motion detector (HR-EMD) (Hassenstein and Reichardt 1956). The HR-EMD uses two spatially separated contrast signals and correlates them after a delay (figure 2). In our model, the HR-EMD was applied as a 2nd-order motion detector on the ESTMD (1st order motion detector) outputs (via a low-pass filter, $\tau_{\text{HR-EMD}} = 40 \text{ ms}$) resulting in a direction selective output. Although the HR-EMD confounds spatial attributes of the target (e.g. size in the direction of travel) it is also tuned to the velocity of the pre-filtered ‘small targets’ (Wiederman and O’Carroll 2013b). The output of HR-EMD is positive when the target moves from S_1 to S_2 (figure 2), and negative in the reverse direction. The HR-EMD was applied in both horizontal and vertical directions to estimate whether the target is moving right/up (positive) or left/down (negative). The spatial component of the target velocity vector was determined by binning the magnitude of the output of the HR-EMD into three equal intervals, to estimate whether the speed of the target is ‘slow’, ‘medium’ or ‘fast’ (Bagheri et al 2015a), a strategy similar to that observed behaviourally in crabs (Nalbach 1989).

2.2. Saccadic pursuit algorithm

Flying insects use various pursuit strategies to control their forward velocity and distance, whilst fixating the target in the frontal visual field. For example, a male housefly uses a 0° ‘tracking’ strategy to chase another fly, resulting in complex looping pursuit paths (Land and Collett 1974, Wehrhahn et al 1982). An aerial predator, such as a perching dragonfly, uses

an ‘interception’ strategy that maintains the prey at a fixed relative bearing (Mischiati et al 2015). Inspired by these strategies, we implemented a hybrid pursuit mode (Bagheri et al 2015a), where the robot initiates a frontal fixation saccade whenever the winning feature of the ESTMD output moved more than 5° from the centre of the field of view. This strategy keeps the target close to the pole of expansion in the flow-field generated by the pursuer’s own progressive motion through the world, i.e. where local background image speeds are lowest. The fast adaptation mechanisms in the earlier visual processing then enhance target ‘pop out’ against a highly cluttered background during the inter-saccade period.

在“turn”的过程中又回到小目标通过检测

2.3. Experimental setup

The robotic platform was a Husky A200 (Clearpath Robotics™) unmanned ground vehicle which uses an open source serial protocol. The development framework for this robot was robot operating system (ROS). A Blackfly camera (BFLY-U3-13S2C-CS, Point Grey Research Inc) with a CS mount 1/3" sensor ($53^\circ \times 100^\circ$ sized viewport) was mounted on the robot to capture videos of the environment (figure 1). Due to technical limitations of the camera, video was sampled at 20 Hz to represent the visual field of the robot, which moved at a velocity of 0.1 m s^{-1} . Although real-time, our autonomous system operated in a ‘slowed down’ environment (limited by the camera frame rate) with tracking of the output target location at a corresponding 20 Hz. Different size and colour foam balls were used as targets (see table 1 for detailed parameters). The balls were fixed to a thin transparent line, wrapped around a motorized driving pulley (figure 3). Two motor speeds were tested, resulting in target velocities of either 0.06 m s^{-1} (‘slow’) or 0.12 m s^{-1} (‘fast’). The target track was mounted at a height which varied between 50–150 cm above the ground. Five idler turning pulleys changed the direction of the target path (figure 3). Six different paths were tested for each set of environmental and model parameters. The pursuit was scored as a success if the robot passed within 1 m of the frontally fixated target, before the target completed one cycle.

Experiments were conducted both in an indoor environment under controlled conditions and in unstructured outdoor environments. For indoor experiments, images or videos of natural scenes (figures 4(a) and (b), Movie 1, and Movie 2 of the supplementary material) were projected (2 projectors) onto a wall as a backdrop for the target (image statistics, table S1). Outdoor experiments were conducted in four different locations at different times during the day throughout a month. Figure 4(c) shows images of these locations taken by the mounted robot camera.

3. Results

3.1. Indoor experiments

3.1.1. Effect of facilitation kinetics on pursuit success. Previous modelling efforts highlighted that optimum temporal parameters for facilitation (i.e. the duration of the enhanced region around a selected target) should be dynamically

Table 1. Target size and colours used for different experiments.

Target	Colour	Black		Dark grey		Medium grey		Light grey		White	
	Diameter (mm)	65	100	65	100	65	100	65	100	65	100
Experiment	Indoor	✓	✓	✓		✓					
	Vibration	✓	✓					✓			
	Outdoor		✓		✓			✓		✓	✓

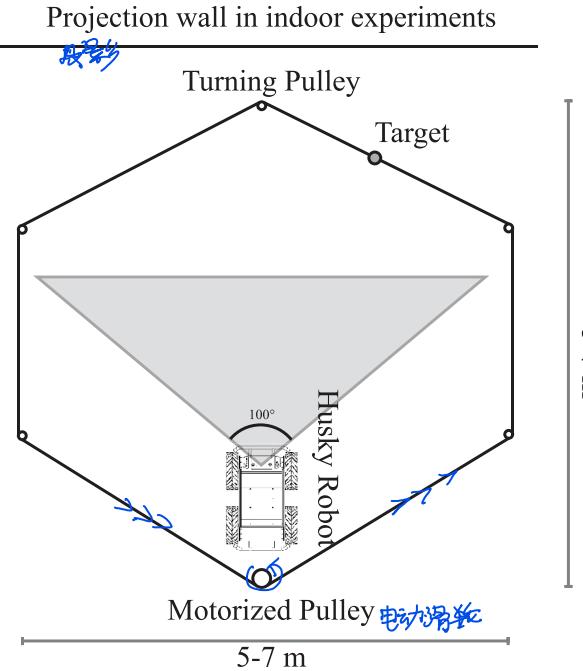


Figure 3. Experimental setup. A monofilament fishing line, wrapped around a motorized driving pulley moves the target along the track.

modulated based on the amount of background clutter and the target velocity (figure S1 (stacks.iop.org/JNE/14/046030/mmedia) and Bagheri *et al* 2015a). To validate simulation results and test our hardware implementation, we conducted indoor robotic experiments by projecting the same natural images onto the wall (figure 4(a)).

Figure 5 shows the pursuit success rate averaged over the four targets used in these experiments (varying size and colour, table 1). As in our previous simulations (figure S1), images that include either naturalistic ('Botanic') or urban ('Forecourt') clutter, were more likely to evoke false positives. In contrast, sparse images ('Field') or those composed predominantly of straight edges ('House'), elicited fewer false positives. Consequently, *Field* and *House* have higher maximum average success rates than *Botanic* and *Forecourt*.

Although projecting images on the wall results in lower contrast background features, we observed similar results to those described in our previous VR simulations (Bagheri *et al* 2015a). In all but the sparsest scene (*Field*), as target velocity increased the optimal time constant decreases (figure 5, see red and green lines). A lower time constant is required to 'keep up' with the faster moving target. Additionally, the robot experiments show that the optimal facilitation time

constant changes across background images. At either target speed, pursuit success improves with a longer time constant in cluttered images (*Botanic* and *Forecourt*), compared to sparser images (*Field* and *House*). This reveals that a longer facilitation time constant enhances the region around a camouflaged target for a longer duration, thus permitting reacquisition.

3.1.2. Sensitivity to vibration. A challenge for visual target-tracking from a mobile platform is dealing with motion blur and uncertainty in target location arising from environmental forces (e.g. wind) and vibration (Irani *et al* 1992). To quantify the effect of vibration, we tested the robot on two artificially created, uneven surfaces (figure 6(a)) and compared the results with a flat surface. The first ('Surface 1') includes numerous small obstacles (up to 30 mm) taped to the floor to generate brief bumps, whilst *Surface 2* includes both bumps and 15–30 mm stones randomly scattered.

Figure 6(b) shows the spectral density of the surface-induced target displacement (robot heave/pitch and yaw) in the output of the camera. The target location in the input image was determined manually which results in low amplitude noise (stationary robot). The *Flat Surface* condition provides a baseline measure of vibration and disturbances arising from robot components (torque timing belt and wheel tread). *Surface 1* causes high amplitude transient events in heave/pitch but does not have any significant effect on yaw. *Surface 2* induced significant mid-frequency (1–3 Hz) vibration on both heave/pitch and yaw motion.

Figure 7 shows that pursuit success varies for different surfaces. *Surface 1* slightly reduces the robot efficacy compared to *Flat Surface* (~8% at optimum time constant) due to the low frequency disturbances. However, as the difficulty of the surface increases (*Surface 2*) the effect of vibration becomes more prominent. The motion blur and uncertainties in target location caused from significant yaw events results in up to 25% reduction of pursuit success compared to *Flat Surface*. Interestingly, the optimum facilitation time constant decreases for *Surface 2*, meaning that a faster facilitation mechanism is required to keep up with the frequent changes of target location in the camera output.

3.2. Outdoor experiments

We were able to control environmental parameters (i.e. illumination, clutter, vibration) in our indoor experiments and test their effect on robot performance. However, natural environments are very dynamic and the pursuer must deal with these

Fig b
振动
抖动



Figure 4. Backgrounds for experiments (a) images and (b) snapshots of videos of natural environments projected onto the wall in indoor experiments. (c) Video output of robot showing the environmental conditions in each outdoor experimental location.

challenges. To examine model performance in unstructured environments, we set our robot to run autonomously in several outdoor locations. An example of the robot footage as well as a video output of robot can be seen in supplementary material (supplementary movie 3 and movie 4, respectively). Examples of robot trajectories in the experiments are shown in figure S2.

3.2.1. Contrast sensitivity in open-loop simulations. Illumination has a significant impact on the appearance of surfaces, as specular reflections and shadows change. This imposes an additional challenge when testing the influence of model parameters on target-tracking success in unstructured environments and elucidating causes of pursuit failure. One way to deal with this problem is to investigate correlations between target contrast and model performance.

To measure the contrast sensitivity of our model, we simulated an immobilized pursuer viewing targets of varying contrast drifting horizontally against a white background (for 550 ms). The data (figure 8(a)) show that the addition of facilitation substantially increases model contrast gain. With a fast facilitation mechanism ($\tau_f = 40$ ms), the target contrast required to evoke 50% maximal response (C50) is very low (~0.15). However, as the time constant increases the sensitivity to low contrast targets decreases, such that C50 for the

most sluggish facilitation time constant ($\tau_f = 2000$ ms) is 0.38. The C50 increases to approximately 0.42 for the non-facilitated model and the model never reaches the maximum response. In all cases, the model does not respond to targets with contrasts equal or lower than 0.1.

The addition of a facilitation mechanism clearly increases the contrast sensitivity, but is the strength of this enhancement dependent on the strength of the facilitating (priming) target? To answer this question, we started the simulation with a stimulus of a low (0.2), medium (0.5) or high (1) contrast (primer) and varied the stimulus contrast after 200 ms (Target in figure 8(b)). Figure 8(b) shows the average model responses to the tested target contrasts for a 20 ms interval immediately after priming.

Facilitation mechanisms with a short time constant build up faster and elicit higher responses. In the presence of a primer, facilitation builds prior to the contrast variation, thus improving the minimum contrast sensitivity (the model responds to a target contrast of 0.1). Interestingly, the low and medium contrast primer elicit a higher response than the high contrast primer, as also observed in physiological experiments (personal communication). This peculiarity of the contrast sensitivity functions observed in both modelling and physiology, emerges from the combined effects of fast temporal adaptation (ESTMD stage) and facilitation.

fig 8A

对比敏感度
感受性
敏感度

fig 8B

??

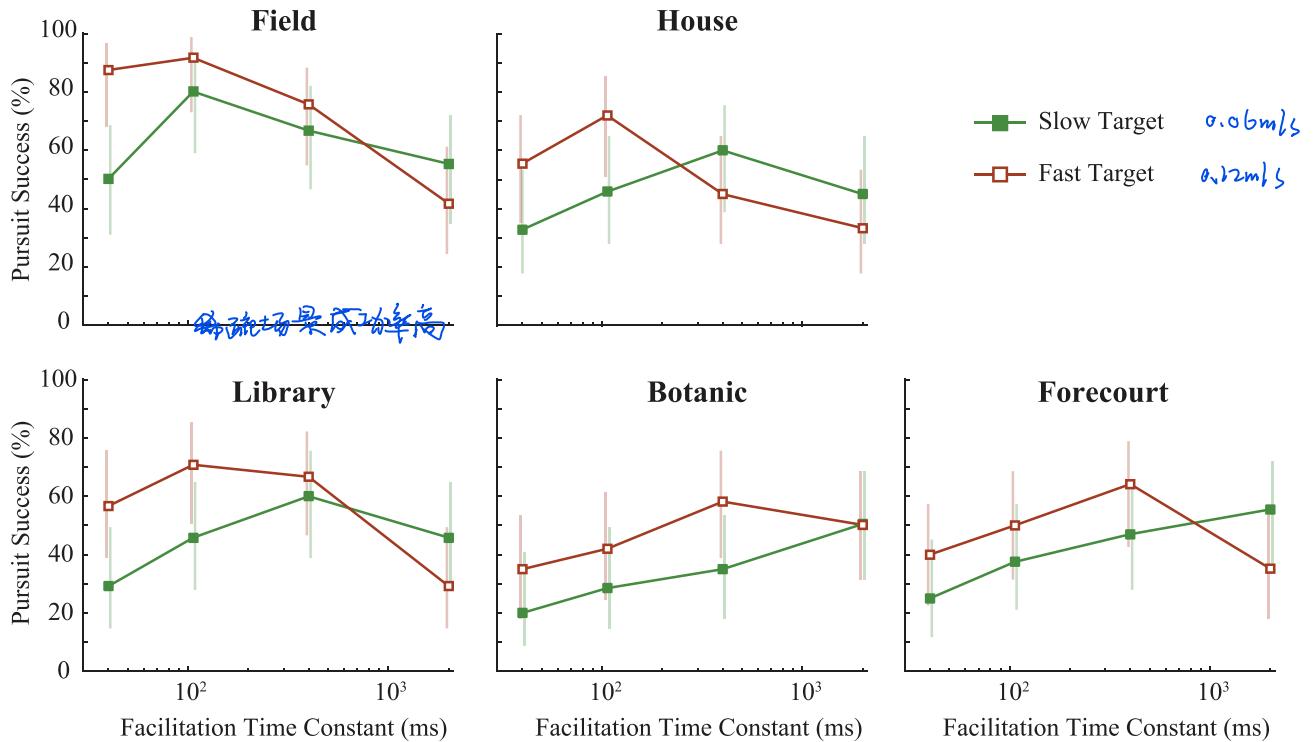


Fig 5. Pursuit success of indoor experiments against projected natural scenes for two target velocities (0.06 m s^{-1} , 0.12 m s^{-1}) with changes in facilitation time constant ($\pm 95\%$ CI, adjusted Wald, $n = 24$) across target contrasts ranging from high to low (table 1). As expected, the robot has a higher pursuit success when tracking targets against less cluttered scenes (e.g. field). These results show that the optimum facilitation time constant varies, dependent on both target velocity and the background scene.

3.2.2. Contrast sensitivity in closed-loop robotic experiments. Targets in natural scenes vary in contrast which may induce an attentional ‘switch’ to a false positive in the scene, consequently resulting in pursuit failure. Figure 9(a) shows box-and-whiskers plots summarizing the average target contrast during pursuits (C_T , $n = 120$). The central mark (red line) is median of average contrast, edges are the 25th and 75th percentiles, and whiskers are the non-outlier data range. Using our robotic platform, we quantified the effect of target contrast in closed-loop pursuits. Average target contrast during pursuits (C_T , figure 9(a)) at the model input stage (following optical blur) were segmented into five bins and plotted against pursuit success (figure 9(b)). Unsurprisingly, high contrast targets result in high capture success (~100% at $0.4\text{--}0.5 C_T$). When target contrast is low, changes in facilitation time constant have little effect, due to detection failure. The largest effect of facilitation time constant is when target contrast is greater than 0.3. However, unlike the results of our contrast sensitivity (section 3.2.1) a shorter time constant is not necessarily beneficial. This reflects the effect of target velocity and background image statistics on the optimum facilitation time constant (section 3.1.1).

The robot can succeed during pursuit of low contrast targets ($C_T < 0.1$), albeit at a low rate (~10%). Because target contrast changes during pursuits (dependent on background and overall illumination), it is feasible that facilitation builds in response to a high contrast target and ‘locking-on’ to a target that decreases in contrast later in the pursuit (section 3.2.1, figure 8(b)).

3.2.3. Overall performance. Figure 10 shows the 2D histograms of input imagery statistics in outdoor robotic experiments and table 2 summarizes the overall performance of our robot with the optimum time constant for each target velocity (*slow* and *fast*). Clutter was measured using the method developed by Silk (1995). Despite the very challenging conditions in our experiments (low contrast in highly cluttered backgrounds) our robot is capable of detecting the target in ~42% and ~36% of the frames for the *slow* and *fast* target respectively. The more successful detection of the slower target is due to the size and velocity tuning properties of our algorithm, which is optimally tuned to target sizes of ~3–4° moving at velocity of ~70–100° s⁻¹ (Bagheri et al 2017). The maximum pursuit success of our autonomous robot is 56.7%, similar to our previously reported simulation results against images with comparable statistics (i.e. *Library*, *Forecourt*, and *Botanic*, see Bagheri et al (2015a), supplementary material table S1, and figure S1). Impressively, this close similarity in the results is despite the challenges that exist in real-world conditions compared to the idealized simulation signal. This illustrates the robustness of this model when dealing with real-world challenges such as illumination variation, occlusions, presence of distractors and direct sunlight.

3.2.4. Effect of internal models on target detection. During flight, insects make saccadic head movements to keep their target at a specific angular position on the eye (Land and Collett 1974, Wehrhahn et al 1982, Mischiati et al 2015). However, these saccadic movements cause frequent and

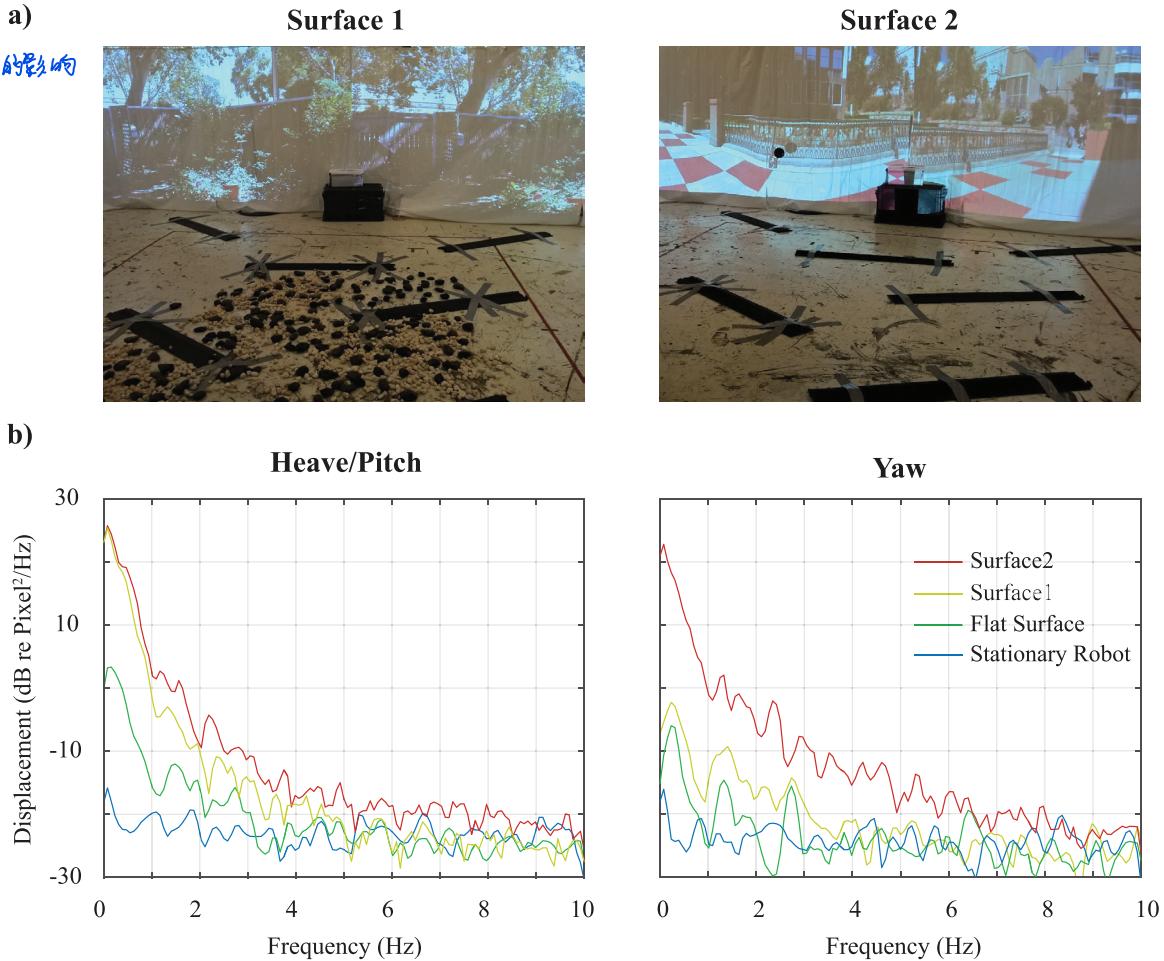


Figure 6. Vibration sensitivity. (a) Two artificially created uneven surfaces that were used to quantify the effect of vibration on model performance. (b) Spectral density of target displacement in the output of camera, resulting from heave/pitch and yaw vibration of the robot.

substantial displacement of the retinal image. Thus, the movements require an anticipatory shift of visual attention from the pre-saccadic to post-saccadic locations. Such prediction and planning, essential to the high-performance control of behaviour, require internal models. It was recently discovered that flying insects rely on such internal models to guide actions (Kim *et al* 2015, Mischiati *et al* 2015).

We tested the effect of internal models on target tracking by feeding video captured by the robot camera ($n = 20$) into an open-loop version of our target tracking model. The closed-loop robotic implementation allows predictive feed-forward relocation of the facilitation map to the post-saccadic location based on motor outputs. However, such information is unknown to the open-loop model, thus requiring both detection of the target and establishment of facilitation at the new post-saccadic location. Figure 11(a) shows that the median of successful detection in the open-loop system drops to 48% compared to 59% in the closed-loop scenario, thus showing the essential role of internal models in target detection in tracking.

3.2.5. Facilitation and attention. Previously, we proposed a role for facilitation in the selective attention (Bagheri *et al* 2015b) observed in dragonfly CSTMD1 neurons (Wiederman

and O'Carroll 2013a). This selection could be induced by a facilitation mechanism increasing contrast sensitivity around one target (section 3.2.1), concomitant with surround suppression. We tested the effect of increased contrast sensitivity on target detection and tracking in natural environments and in the presence of distractors by using the model in open-loop. We used video imagery captured from the robot camera ($n = 10$) in which the model struggles to detect the target in the early stages but locks on to it later during the pursuit (e.g. supplementary material, movie 4). These videos served as input to the open-loop simulations. Prior to the start of these simulations, we allowed the facilitation to build up in the initial target location for either 200 or 500 ms (primed). This was implemented by artificially feeding the target location in the first frame as the future location of the target ($r'(t+1)$ in figure 1) to the facilitation mechanism. We measured the successful target detection within the frames prior to the model lock-on to the target. Figure 11(b) shows the difference between the primed (open-loop) and un-primed (closed-loop robotic experiments) model. The 200 ms and 500 ms primed facilitation increase the median of successful target detection to 29% and 34% compared to 3% in un-primed scenarios. These results show that presence of facilitation can direct the attention to target location irrespective of the presence of other distractors.

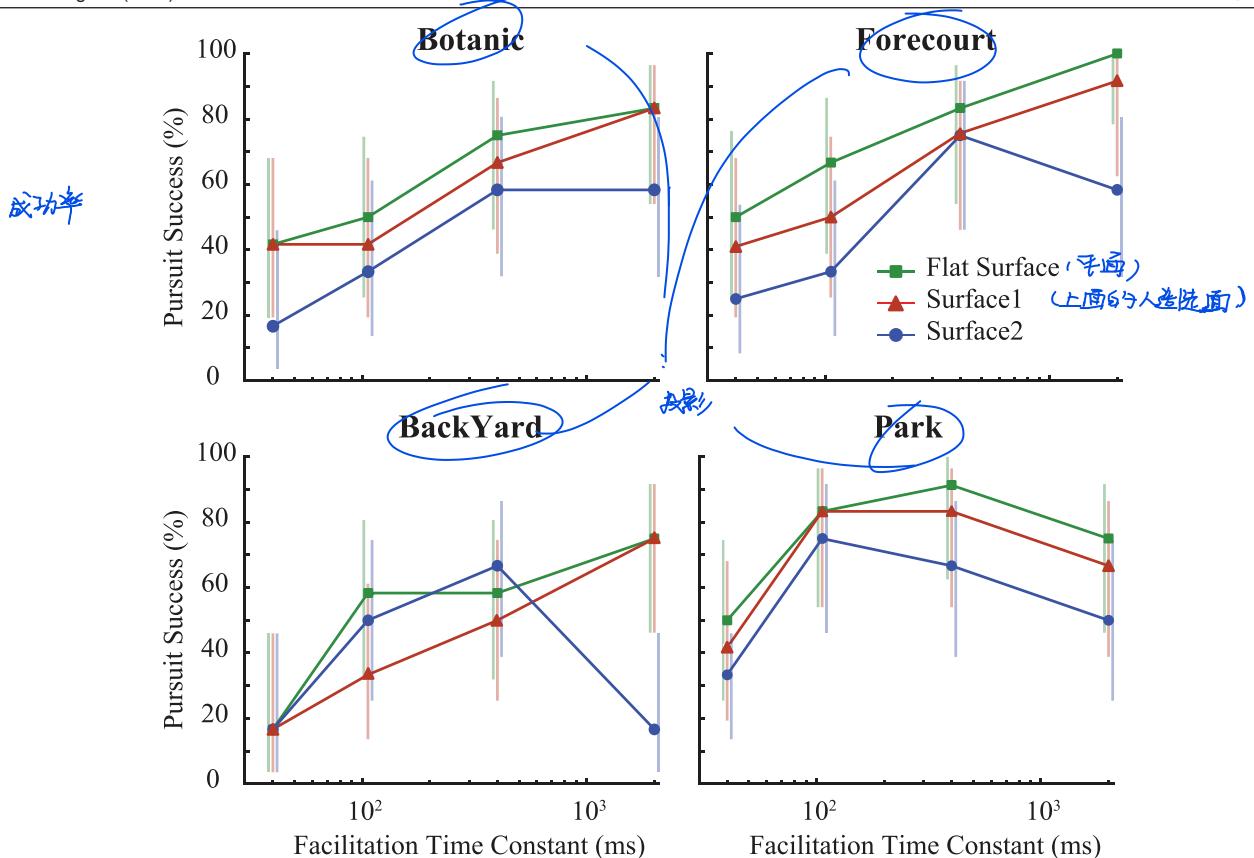


Figure 7. Effect of vibration on robot performance. Presence of uneven surfaces degrades performance ($\pm 95\% \text{CI}$, adjusted Wald, $n = 12$). For Surface 2, a shift towards shorter time constants permits the model to withstand sudden changes in target location arising from robot vibration.

提高对振动的敏感性:

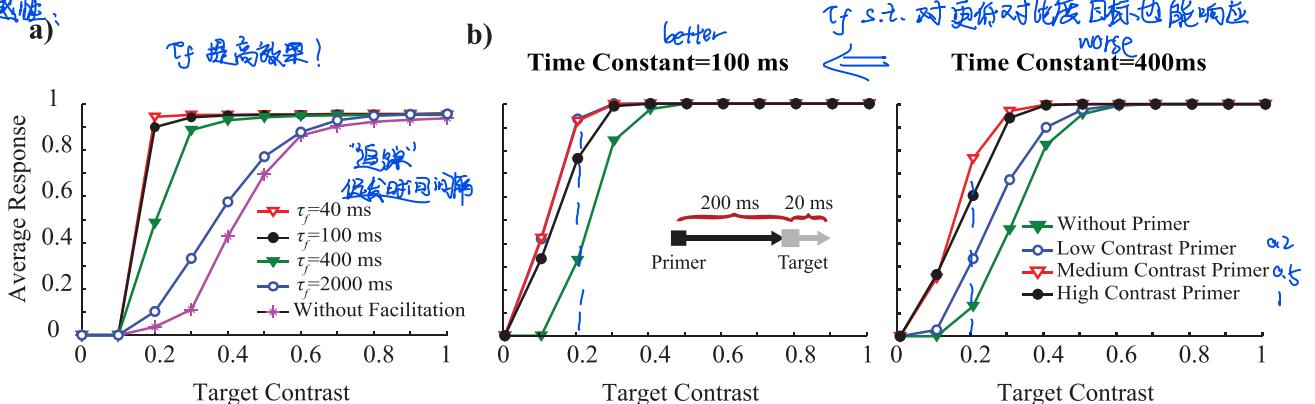


Figure 8. Contrast sensitivity of the model (a) open-loop model response increases as target contrast increases (purple line). The addition of facilitation (at various time constants) increases contrast sensitivity. However, there is a hard threshold at a target with contrast of 0.1. (b) Targets of varying contrast were preceded by either a low (blue), medium (red) or high (black) contrast primer. Facilitation increases model contrast sensitivity and threshold.

4. Discussion

Our recent benchmarking study (Bagheri *et al* 2017) demonstrated that when tracking small moving targets in natural scenes (using open-loop simulations), our insect-inspired model exhibits robust and efficient performance, outperforming state-of-the-art tracking algorithms. The success of these simulations led us to test the efficacy and robustness of our autonomous hardware platform, within a complex, natural environment. Our data show that this system can effectively handle noise from a variety of sources (e.g. vibration,

illumination) and can successfully track targets despite the challenging experimental conditions, such as, low target contrast, heavily cluttered environments and the presence of distractors.

4.1. Facilitation time constant

Using closed-loop simulations we previously showed that the optimum choice of facilitation time constant depends on both target velocity and background clutter (Bagheri *et al* 2015a). The results of our closed-loop robotic experiments suggest a

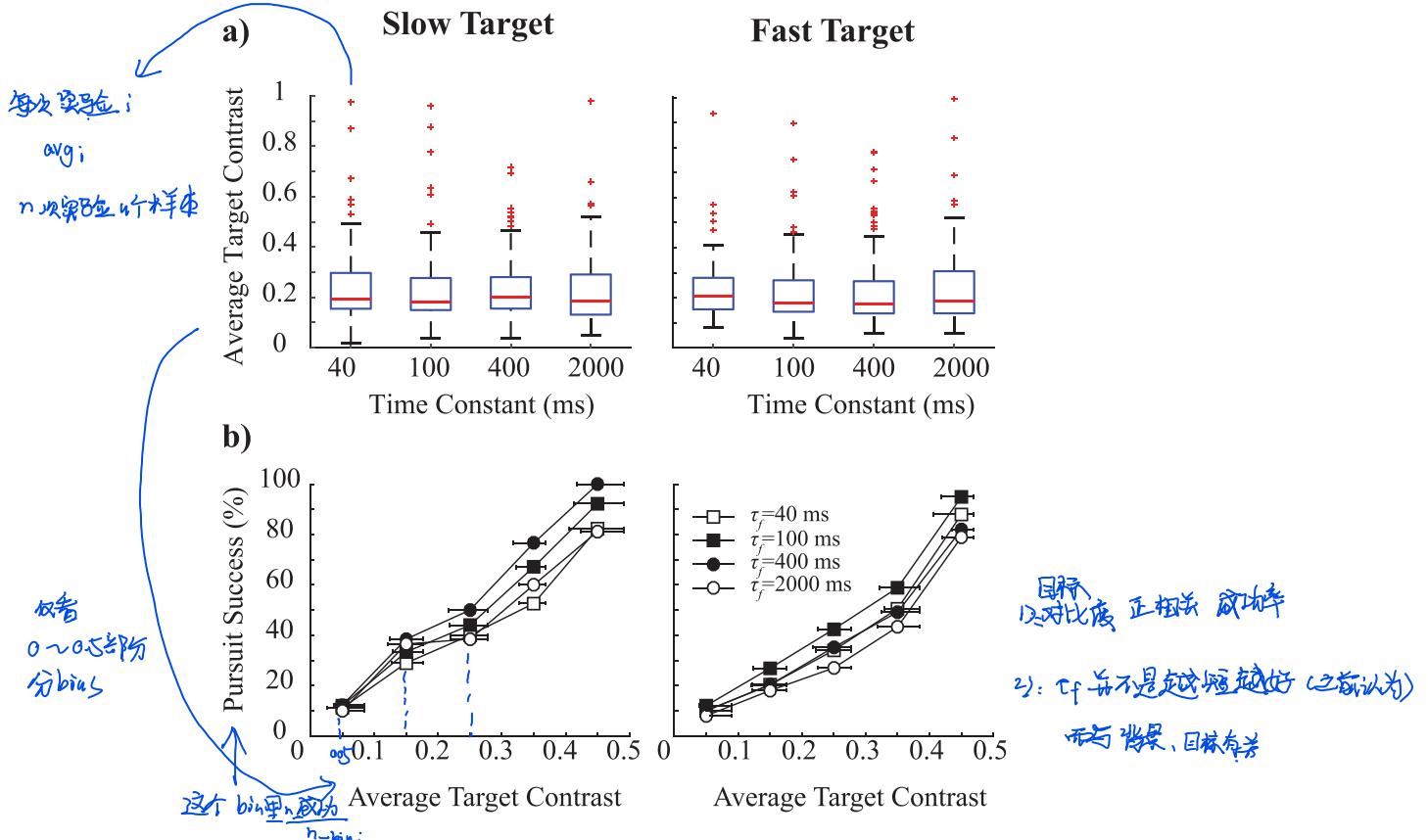


Figure 9. Effect of contrast on closed-loop robotic target tracking. (a) The range of average target contrast during experiments (C_T , $n = 120$). Although illumination, and therefore target contrast, changes during experiments, the median of average contrast is similar for different experimental parameters (i.e. time constant and target velocity). (b) The average target contrast during pursuits were organized into five bins with 0.1 contrast intervals and the percentage of successful pursuits in each bin was calculated. The error bars show the deviation of contrast from the centre of each bin.

similar relationship. Here we used several variants of facilitation time constant to find the optimum. In future robotic development, we aim to dynamically estimate the facilitation time constant, using real-time estimates of target velocity and background clutter. Given the efficiency of our model (Bagheri *et al* 2017) such a dynamic modulation may increase the robustness of pursuit without affecting the stability of the feedback process. However, from a physiological perspective, determining whether STMD neurons use such a dynamic modulation requires further experimentation.

4.2. Velocity estimation

We predicted the target's future location using an estimate of current target velocity, because our most recent physiological data indicates such a velocity dependency (unpublished observations). Rather than calculate a continuous velocity range, we used an HR-EMD model to categorize the target velocity as either 'slow', 'medium', or 'fast' speed. Similar banding into separate channels (temporal frequency) has been observed to underlie velocity estimation in crabs (Nalbach 1989). Although the output of HR-EMD is a function of the velocity of the moving stimulus, this relationship is not monotonic and has a strong dependence on spatial structure and contrast of the stimulus. These shortcomings have led to elaborations of the original HR-EMD (Zanker *et al* 1999, Rajesh *et al* 2005,

Brinkworth and O'Carroll 2009). We hypothesised that our model's coarse spatial size of the facilitation matrix (15° by 15° area) would accommodate errors resulting from the texture dependency of the HR-EMD. However, in future work we will incorporate improved velocity estimator methods, derived from our developing understanding of the physiological system. Such methods may include elaborated HR-EMD or time-of-travel models (Roubieu *et al* 2013, Sabiron *et al* 2013, Vanhoutte *et al* 2017) and we will test their impact on the target tracking model.

4.3. Effect of vibration on target tracking

Whether flying, walking, or swimming, animals maneuvering in natural environments must deal with forces and vibration from uneven terrain or turbulence (in air or water). Vibration can impair the acquisition of information (e.g. by the eyes), the outcome of motor command of information (e.g. head or body movements) or the complex central processes that relate input sensory information to the output motor command.

The results show that our model can robustly track targets even in the presence of vibration. As vibration-induced target displacement increases (e.g. Surface 2 in figure 6(a)), a shorter facilitation time constant (on the order of 100–400 ms) improves the robustness of tracking. This match for the physiologically measured facilitation time (on the order of

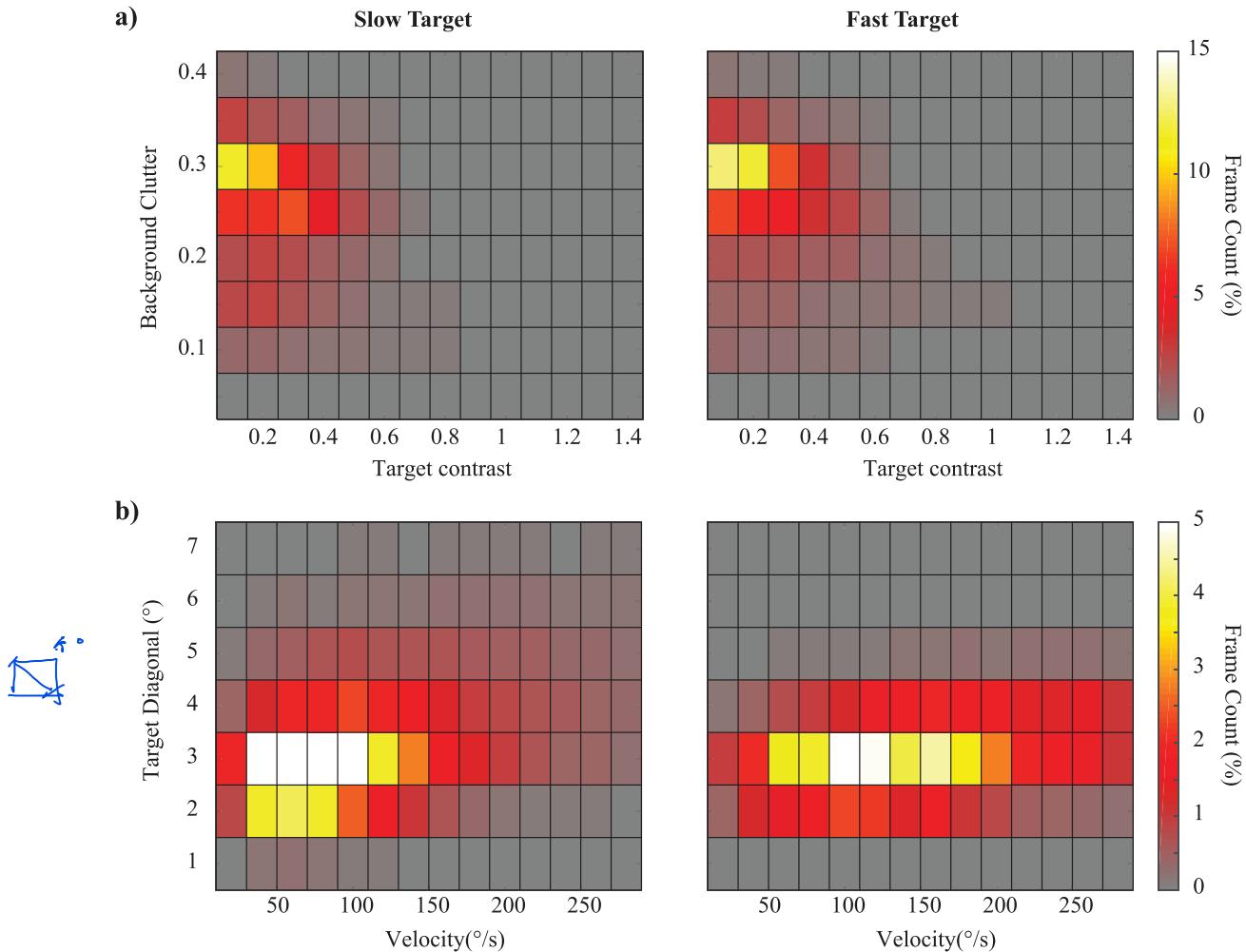


Figure 10. 2D histogram of input imagery statistics in outdoor experiments showing (a) background clutter and target contrast (b) the target size and velocity in the video output of the camera. Our size and velocity tuned model responds optimally to targets of $\sim 3\text{--}4^\circ$ moving at a velocity of $\sim 70\text{--}100 (\text{° s}^{-1})$ (Bagheri *et al* 2017).

300–500 ms) reported in our earlier work (Dunbier *et al* 2011, 2012, Nordström *et al* 2011) might reflect the evolution of a facilitation time constant in flying insects that allows them to deal with turbulent air and movement of the head induced by wing movements, while tracking prey or conspecifics.

The effect of vibration on vision may be decreased by reducing its transmission to the head/compound eye. Studies of fly behavior show that they control their direction of flight along with gaze through short, fast saccadic movements where head and body turn independently (Schilstra and Van Hateren 1999). This uncoupling of the eye from its support enables the insect to maintain the orientation of the gaze even when disturbances occur which affect its body. Moreover it reduces the temporal blurring effects and may promote ‘popout’ of a target against a background as a result of the high-pass filtering at early stages of visual processing. Future robotic efforts will investigate the effect of such ‘active vision’ on handling vibration.

4.4. Internal models

Most animals with good vision show a pattern of stable fixations with fast saccades that shift gaze direction (Land

Table 2. Summary of experimental results for the optimum facilitation time constants. (τ_{best}) (τ_{optimal})

Measure	Target speed	
	Slow	Fast
Average Target Contrast	0.24	0.26
Average Background Clutter	0.28	0.27
Total Number of Frames	147828	110103
Successful Frame (%)	41.9	36.4
Pursuit Success (% \pm 95%CI, adjusted Wald, $n = 120$)	56.7 ± 8.7	44.2 ± 8.7
Average Successful Pursuit Time (s)	52	64

结论：成功率高且稳定，成功率相近 = model robust and Collett 1974, Land 1999, Findlay and Gilchrist 2003). An essential component of successful target tracking is the ability to distinguish self-induced motion (such as rotation of the visual field caused by saccadic movement) from those imposed by the environment (e.g. vibration). When an insect drifts from its flight trajectory (due to environmental factors), the optomotor response maintains aerodynamic stability and compensates the animal’s deviation from its initial flight trajectory (governed by an inner-loop control system). However,

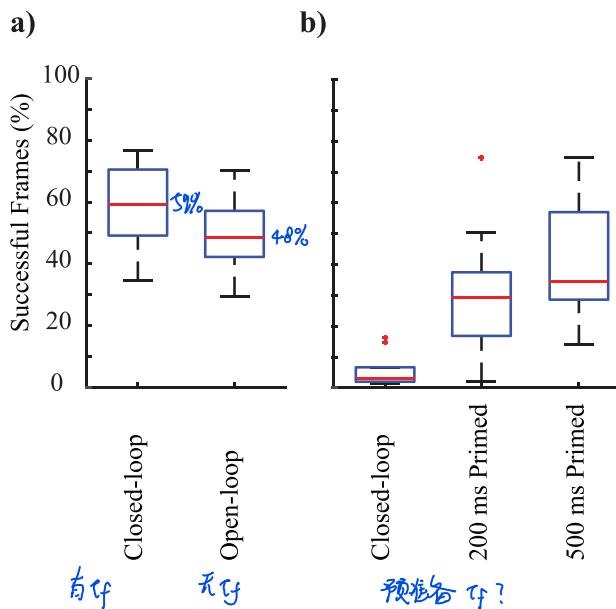


Figure 11. (a) Effect of internal models on target detection. The closed-loop model predicts the new location of facilitation mechanism during saccades based on motor outputs while the open-loop model does not include the internal model of the sensorimotor system. (b) Facilitation mechanism enhances the contrast sensitivity and therefore target detection in the presence of background clutter and distractors. The 200 ms and 500 ms primed facilitation mechanism increases successful detection of the target compared to un-primed closed-loop experiments.

performing voluntary manoeuvres by the insect requires interaction between the control of visual reflexes (inner-loop) and other visually guided behaviours (outer-loop), otherwise the animal would be trapped by its inner-loop control system (von Holst and Mittelstaedt 1950). The question is how the inner-loop optomotor pathway and an outer-loop pathway involved in chasing behaviour may interact? Although different interactions between inner-loop and outer-loop are proposed, recent studies (Kim *et al* 2015, Mischiati *et al* 2015) support a method postulated by von Holst and Mittelstaedt (1950). von Holst and Mittelstaedt (1950) proposed that with each motor command to initiate a voluntary locomotor turn, a copy of the motor command is sent to the visual system (efference copy), a concept similar to forward models in human motor control.

An important feature of forward modelling is that system outputs modulate sensory processing. Therefore, the visual system is not a feed-forward model driven by the sensory input alone, rather motor outputs are required to predict expected visual input. Our results show a significant improvement in target detection and tracking when an internal model is compared to a feedforward model. However, implementation of internal models remains an uncommon approach in artificial vision systems.

4.5. Dynamics of the robot

Dragonflies are light, swift and agile animals with flight speeds up to 6.8 m s^{-1} (Dean 2003). Robust detection of targets at such high velocities requires a temporal resolution close to what is observed in flying insect photoreceptors (100–300

Hz) (Niven *et al* 2007). In the current study, robot and target velocities were limited due to the low temporal frequency of the camera. That is, the slow-moving, ground-based robotic platform does not deal with the same level of dynamic energy and motion control difficulties as experienced by dragonflies. However, the ground-based platform allowed us to address algorithmic questions and avoid the complexities associated with unmanned aerial vehicles (UAVs).

Given the robust performance of our model under real-world conditions, its high processing speed and low computational complexity (Bagheri *et al* 2017), we will now turn to a UAV platform with a high-speed camera and field-programmable gate array (FPGA). To account for the faster dynamics of both predator and prey, we will modify (and test) tuning parameters accordingly. For integration of the stability and guidance of the UAV, an inner-loop control system can be exploited to constantly maintain the UAV's attitude in conjunction with its aerodynamic stability by compensating for any deviations in roll, pitch, and yaw. However, during a saccadic movement the outer-loop simply can change the set point of the inner-loop control system allowing performance of intended flight manoeuvres while keeping the inner-loop control active.

Implementation of the model on a UAV with high-speed camera should permit tracking of targets at high velocities. This would allow us to increase the level of noise in the input imagery (due to increase in dynamic energy of the robot) and test question such as the effect of noise reduction in the early visual processing on the model performance. Here, our choice of the time constants for filters replicated parameters observed in day-active insects, however with our robotics platform we will be able to implement a wider range of time constants, such as those observed in nocturnal animals. Thus, our future robotic efforts will attempt to develop a robust fast-moving, UAV platform as well as permit us to address further comparative, physiological questions.

5. Conclusion 做出的贡献 (哪些没说)

While the results of our recently developed insect-inspired target tracking model (Bagheri *et al* 2015a) provide insight into insect neurophysiology, our understanding of animal sensorimotor systems is still limited. Experiments require directly linking neural circuits and behaviour, however, during physiological recordings our insect is restrained with wax and can only experience imposed, open-loop stimuli. To model sensorimotor systems, it is necessary to accurately represent the physical interaction of the animal and the environment which is very complex to model in simulations. To the best of our knowledge, this is the first time that a target tracking model inspired by insect neurophysiology has been implemented on an autonomous robot and tested under real-world conditions. We not only reveal robust model performance, but also provide insight into how insects' neuronal systems may handle varying challenges during target tracking and pursuit. That is, our hardware implementation provides a platform for better understanding the sensorimotor system of the insect as well as a prototype for engineering applications.

Acknowledgment

This research was supported under the Australian Research Council's Discovery Projects (DP130104572), the Discovery Early Career Researcher Award (DE15010054) funding scheme, and the Swedish Research Council (VR 2014-4904). We thank the manager of the Waite Campus of the University of Adelaide for allowing the robotic experiments.

ORCID

Zahra M Bagheri  <https://orcid.org/0000-0002-1749-3441>
 Benjamin Cazzolato  <https://orcid.org/0000-0003-2308-799X>
 David O'Carroll  <https://orcid.org/0000-0002-2352-4320>
 Steven Wiederman  <https://orcid.org/0000-0002-0902-803X>

References

- Bagheri Z M, Wiederman S D, Cazzolato B S, Grainger S and O'Carroll D C 2014a A biologically inspired facilitation mechanism enhances the detection and pursuit of targets of varying contrast *Int. Conf. Digit. Image Comput. Tech. Appl. (DiCTA)* pp 1–5
- Bagheri Z, Wiederman S D, Cazzolato B S, Grainger S and O'Carroll D C 2014b Performance assessment of an insect-inspired target tracking model in background clutter *Int. Conf. Control Autom. Robot. Vis. (ICARCV)* pp 822–6
- Bagheri Z M, Wiederman S D, Cazzolato B S, Grainger S and O'Carroll D C 2015a Properties of neuronal facilitation that improve target tracking in natural pursuit simulations *J. R. Soc. Interface* **12** 20150083
- Bagheri Z M, Wiederman S D, Cazzolato B, Grainger S and O'Carroll D C 2015b Robustness and real-time performance of an insect inspired target tracking algorithm under natural conditions *2015 IEEE Symp. Series on Comput. Intell. (IEEE)* pp 97–102
- Bagheri Z M, Wiederman S D, Cazzolato B S, Grainger S and O'Carroll D C 2017 Performance of an insect-inspired target tracker in natural conditions *Bioinspir. Biomim.* **12** 025006
- Barnett P D, Nordström K and O'Carroll D C 2007 Retinotopic organization of small-field-target-detecting neurons in the insect visual system *Curr. Biol.* **17** 569–78
- Brinkworth R S and O'Carroll D C 2009 Robust models for optic flow coding in natural scenes inspired by insect biology *PLoS Comput. Biol.* **5** e1000555
- Cai B, Xu X, Xing X, Jia K, Miao J and Tao D 2016 BIT: biologically inspired tracker *IEEE Trans. Image Process.* **25** 1327–39
- Collett T S 1980 Angular tracking and the optomotor response: an analysis of visual reflex interaction in a hoverfly *J. Comp. Physiol.* **140** 145–58
- Colonnier F, Manecy A, Juston R, Mallot H, Leitel R, Floreano D and Viollet S 2015 A small-scale hyperacute compound eye featuring active eye tremor: application to visual stabilization, target tracking, and short-range odometry *Bioinspir. Biomim.* **10** 026002
- Corbet P S 1999 *Dragonflies: Behaviour and ecology of Odonata* (Ithaca, NY: Cornell University Press)
- Dean T J 2003 Fastest flyer *Book of Insect Records* (Gainesville, FL: University of Florida) ch 1 http://entnemdept.ufl.edu/walker/ufbir/chapters/chapter_01.shtml
- Dunbier J R, Wiederman S D, Shoemaker P A and O'Carroll D C 2011 Modelling the temporal response properties of an insect small target motion detector *IEEE Int. Conf. Intell. Sensors Netw. Inf. Process. (ISSNIP)* pp 125–30
- Dunbier J R, Wiederman S D, Shoemaker P A and O'Carroll D C 2012 Facilitation of dragonfly target-detecting neurons by slow moving features on continuous paths *Front. Neural Circuits* **6** 79
- Findlay J M and Gilchrist I D 2003 *Active Vision* (Oxford: Oxford University Press)
- Halupka K J, Wiederman S D, Cazzolato B S and O'Carroll D C 2011 Discrete implementation of biologically inspired image processing for target detection *IEEE Int. Conf. Intell. Sensors Netw. Inf. Process. (ISSNIP)* pp 143–8
- Halupka K J, Wiederman S D, Cazzolato B S and O'Carroll D C 2013 Bio-inspired feature extraction and enhancement of targets moving against visual clutter during closed loop pursuit *IEEE Int. Conf. Image Process. (ICIP)* pp 4098–102
- Hassenstein B and Reichardt W 1956 Systemtheoretische analyse der Zeit-, Reihenfolgen- und Vorzeichenauswertung bei der Bewegungsperzeption des Rüsselkäfers Chlorophanus *Z. Naturforsch. B* **11** 513–24
- Irani M, Rousso B and Peleg S 1992 Detecting and tracking multiple moving objects using temporal integration *European Conf. Comput. Vis.* pp 282–7
- James A C 1990 White-noise studies in the fly lamina *PhD Thesis* The Australian National University
- Jansonius N M and Van Hateren J H 1991 Fast temporal adaptation of on-off units in the first optic chiasm of the blowfly *J. Comp. Physiol. A* **168** 631–7
- Kim A J, Fitzgerald J K and Maimon G 2015 Cellular evidence for efference copy in Drosophila visuomotor processing *Nat. Neurosci.* **18** 1247–55
- Krapp H G and Wicklein M 2008 Central processing of visual information in insects *The Senses: A Comprehensive Reference* vol 1 (New York: Academic) pp 131–203
- Land M F 1997 Visual acuity in insects *Annu. Rev. Entomol.* **42** 147–77
- Land M F 1999 Motion and vision: why animals move their eyes *J. Comp. Physiol. A* **185** 341–52
- Land M F 2015 Eye movements of vertebrates and their relation to eye form and function *J. Comp. Physiol. A* **201** 195–214
- Land M F and Collett T S 1974 Chasing behaviour of houseflies (*Fannia canicularis*) *J. Comp. Physiol.* **89** 331–57
- Mahadevan V and Vasconcelos N 2013 Biologically inspired object tracking using center-surround saliency mechanisms *IEEE Trans. Pattern Anal. Mach. Intell.* **35** 541–54
- Mischiatini M, Lin H T, Herold P, Immer E, Olberg R and Leonardo A 2015 Internal models direct dragonfly interception steering *Nature* **517** 333–8
- Nalbach H O 1989 Three temporal frequency channels constitute the dynamics of the optokinetic system of the crab, *Carcinus maenas* (L.) *Biol. Cybern.* **61** 59–70
- Niven J E, Anderson J C and Laughlin S B 2007 Fly photoreceptors demonstrate energy-information trade-offs in neural coding *PLoS Biol.* **5** e116
- Nordström K, Barnett P D and O'Carroll D C 2006 Insect detection of small targets moving in visual clutter *PLoS Biol.* **4** e54
- Nordström K, Bolzon D M and O'Carroll D C 2011 Spatial facilitation by a high-performance dragonfly target-detecting neuron *Biol. Lett.* **7** 588–92
- Nordström K and O'Carroll D C 2009 Feature detection and the hypercomplex property in insects *Trends Neurosci.* **32** 383–91
- O'Carroll D 1993 Feature-detecting neurons in dragonflies *Nature* **362** 541–3
- O'Carroll D C, Barnett P D and Nordström K 2011 Local and global responses of insect motion detectors to the spatial structure of natural scenes *J. Vis.* **11** 20
- O'Carroll D C and Wiederman S D 2014 Contrast sensitivity and the detection of moving patterns and features *Phil. Trans. R. Soc. B* **369** 20130043

- Olberg R M, Worthington A H and Venator K R 2000 Prey pursuit and interception in dragonflies *J. Comp. Physiol. A* **186** 155–62
- Osorio D 1991 Mechanisms of early visual processing in the medulla of the locust optic lobe: how self-inhibition, spatial-pooling, and signal rectification contribute to the properties of transient cells *Vis. Neurosci.* **7** 345–55
- Rajesh S, O'Carroll D and Abbott D 2005 Man-made velocity estimators based on insect vision *Smart Mater. Struct.* **14** 413
- Riesenhuber M and Poggio T 1999 Hierarchical models of object recognition in cortex *Nat. Neurosci.* **2** 1019–25
- Roubieu F L, Expert F, Sabiron G and Ruffier F 2013 Two-directional 1 g visual motion sensor inspired by the fly's eye *IEEE Sens. J.* **13** 1025–35
- Sabiron G, Chavent P, Rahariaona T, Fabiani P and Ruffier F 2013 Low-speed optic-flow sensor onboard an unmanned helicopter flying outside over fields *IEEE Int. Conf. Robot. Autom. (ICRA)* pp 1742–9
- Schilstra C and Van Hateren J H 1999 Blowfly flight and optic flow. I. Thorax kinematics and flight dynamics. *J. Exp. Biol.* **202** 1481–90
- Silk J D 1995 *Statistical Variance Analysis of Clutter Scenes and Applications to a Target Acquisition Test* (Alexandria, VA: Institute for Defense Analysis) p 2950
- Srinivasan M V, Laughlin S B and Dubs A 1982 Predictive coding: a fresh view of inhibition in the retina *Proc. R. Soc. B* **216** 427–59
- Stavenga D 2003 Angular and spectral sensitivity of fly photoreceptors. I. Integrated facet lens and rhabdomere optics *J. Comp. Physiol. A* **189** 1–17
- Straw A D, Warrant E J and O'Carroll D C 2006 A bright zone in male hoverfly (*Eristalinus*) eyes and associated faster motion detection and increased contrast sensitivity *J. Exp. Biol.* **209** 4339–54
- Vanhoutte E, Mafrica S, Ruffier F, Bootsma R J and Serres J 2017 Time-of-travel methods for measuring optical flow on board a micro flying robot *Sensors* **17** 571
- von Holst E and Mittelstaedt H 1950 Das Reafferenzprinzip. Wechselwirkungen zwischen Zentralnervensystem und Peripherie *Naturwissenschaften* **37** 464–76
- Webb B, Harrison R R and Willis M A 2004 Sensorimotor control of navigation in arthropod and artificial systems *Arthropod Struct. Dev.* **33** 301–29
- Wehrhahn C, Poggio T and Bühlhoff H 1982 Tracking and chasing in houseflies (*Musca*) *Biol. Cybern.* **45** 123–30
- Wiederman S D and O'Carroll D C 2011 Discrimination of features in natural scenes by a dragonfly neuron *J. Neurosci.* **31** 7141–4
- Wiederman S D and O'Carroll D C 2013a Selective attention in an insect visual neuron *Curr. Biol.* **23** 156–61
- Wiederman S D and O'Carroll D C 2013b Biomimetic target detection: modeling 2nd order correlation of OFF and ON channels *IEEE Symp. Comput. Intell. Multimedia Signal Vis. Process. (CIMSIVP)* pp 16–21
- Wiederman S D, Shoemaker P A and O'Carroll D C 2008 A model for the detection of moving targets in visual clutter inspired by insect physiology *PLoS One* **3** e2784
- Zanker J M, Srinivasan M V and Egelhaaf M 1999 Speed tuning in elementary motion detectors of the correlation type *Biol. Cybern.* **80** 109–16
- Zhang S, Yao H and Liu S 2010 Robust visual tracking using feature-based visual attention *IEEE Int. Conf. Acoust. Speech Signal Process. (ICASSP)* pp 1150–3
- Zheng Y and Meng Y 2008 Swarm intelligence based dynamic object tracking *IEEE World Congress. Comput. Intell. Evol. Comput.* pp 405–12