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"**Mechanisms for Visual Detection of Small Targets in Insects**"

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***Note on period of performance:** this report serves as an update to the final reports that we submitted jointly for FA9550-09-1-0116, 10 March 2012, and the interim final report from 20 July 2012 submitted for FA2386-10-1-4114. The project was commenced simultaneously by both PI's in 2009 as a joint, 3-year effort, but this was administered via two separate AFOSR contracts (with the same title and shared reports) and continues as a direct collaboration between the two PI's. However, contracting arrangements for the AOARD-administered funding led to a discrepancy between the performance and reporting periods for the two grants. Throughout the grants, this allowed us to provide more regular updates of progress. This report emphasizes progress achieved by the University of Adelaide research team since we submitted our 'interim' final report in 2012. Further details on outcomes from the earlier reporting periods on both grants are documented in the March 2012 final report for FA9550-09-1-0116.

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14. ABSTRACT
Specialized Small Target Motion Detector Neurons (STMDs) in the optic lobes of the insect brain respond strongly to moving objects even when these are smaller than the nominal resolution limit of the eye. Many STMDs also respond robustly to small targets against complex stationary or moving backgrounds. In the last decade the Principal Investigators on this project have established the underlying neural machinery of STMD system as an important new model system for computational neuroscience and for bio-inspired models of target tracking. With sponsorship from the US Air Force Office of Scientific Research (Contracts F49620-01-C-0030, FA9550-04-1-0283, and Grants FA9550-09-1-0116 and FA2386-10-1-4114), our research has allowed us to characterize and model key physiological properties that underlie the impressive visual abilities of insects such as predatory dragonflies to discriminate and track small moving targets against cluttered backgrounds, despite poor optical resolution (low pixel count). In the process, we have established a foundational literature on this topic.

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1. Abstract:

Background: Specialized Small Target Motion Detector Neurons (STMDs) in the optic lobes of the insect brain respond strongly to moving objects even when these are smaller than the nominal resolution limit of the eye. Many STMDs also respond robustly to small targets against complex stationary or moving backgrounds. In the last decade the Principal Investigators on this project have established the underlying neural machinery of STMD system as an important new model system for computational neuroscience and for bio-inspired models of target tracking. With sponsorship from the US Air Force Office of Scientific Research (Contracts F49620-01-C-0030, FA9550-04-1-0283, and Grants FA9550-09-1-0116 and FA2386-10-1-4114), our research has allowed us to characterize and model key physiological properties that underlie the impressive visual abilities of insects such as predatory dragonflies to discriminate and track small moving targets against cluttered backgrounds, despite poor optical resolution (low pixel count). In the process, we have established a foundational literature on this topic.

Aims & Experiments: In this grant, we hypothesized that these properties required a complex mechanism to avoid breakthrough responses by background features, yet to adequately amplify the weak signal of tiny targets. We combined electrophysiological recording from an identified dragonfly STMD neuron, CSTMD1, with computational modeling of its input pathway (elementary small target motion detectors, ESTMDs). Our data show evidence for responses along long trajectories being strongly facilitated by a mechanism that builds up slowly over several hundred milliseconds. This allows the neurons to give sustained responses to continuous target motion, thus providing a possible explanation for their extraordinary contrast sensitivity. Computational modeling shows that this cannot be accounted for by simple emergent properties of existing bio-inspired motion detector systems. We report here on progress towards understanding the complex operations within the STMD receptive field that explain their extraordinary selectivity. We further developed a discrete time, digital implementation of a complete closed-loop target pursuit system with an ESTMD front end which can be used to evaluate the performance of the ESTMD model as a front end for simulation of target pursuit in visual clutter.

Key findings: We document data exploring two further discoveries based on recordings from the dragonfly CSTMD1 neuron: (1) Evidence that STMDs use a non-linear interaction (as previously hypothesized) between contrast decrements (OFF features) and increments (ON features). This is the first time convincing evidence has been obtained for such an interaction in insect vision, and suggests that STMDs use a fundamentally different underlying mechanism for feature selectivity compared with other biological motion detectors (such as the famous Reichardt EMD model). (2) We further developed several variants of computational models that capture the key properties of direction-selective SF-STMD neurons by cascading partially rectified ESTMD stages with HR-type EMDs, and vice versa. We then examined the key response tuning and predictions of these second order systems for simple stimuli. We found that the combination of an ESTMD front-end with a 2^{nd} order EMD is able to combine both the direction selectivity of classical EMDs with the feature selectivity of the ESTMD model. Moreover, this system explains the stronger dependence on feature contrast in insect STMDs compared with their (EMD based) wide-field motion sensitive counterparts. Finally, this model captures the sharper response tuning for either size or velocity of targets observed in insect STMD neurons compared with the predictions of either EMD or ESTMD models alone.

2. Introduction:

2.1 Background and Objectives

Many animals visualize and track small targets at large distances - be they prey, approaching predators or conspecifics. Insects are an excellent model system for investigating the neural mechanisms that have evolved for this challenging task. Specialized Small Target Motion Detector Neurons (STMDs) in the optic lobes of the insect brain respond strongly to targets that are smaller than the nominal resolution limit of the eye. Such a feature must be blurred to a very low contrast in the retinal image, so its detection and tracking requires enormous *contrast gain*. Many STMDs also respond robustly to small targets against complex stationary or moving backgrounds, which further complicates the task of detecting the feature, since this background clutter both reduces absolute contrast and adds conflicting cues from other contrasting features of the background image.

In this grant, we originally hypothesized that the extraordinary abilities of STMDs stem from a complex mechanism to avoid breakthrough responses by background features, yet to adequately amplify the weak (blurred) signal produced by tiny targets. The primary objective was to improve understanding of the computational principles that underlie the response characteristics of wide-field Small Target Motion Detector neurons in the insect visual system (STMDs). A secondary objective was to achieve a more in-depth empirical characterization of the cellular (neuron) response, particularly with regard to details that bear on the limits of performance as small moving target detectors, and on unresolved questions regarding the underlying computational mechanisms of the biological STMD system. Our original Aims were as follows:

AIM 1. **Rectifying Transient Cells:** The goals were to determine whether or not neurons of this class in fact lie on the neural pathway leading to STMDs; to obtain a more detailed characterization of physiology and anatomy, and to perform modeling and analysis that accounts for details of the physiology and the putative role of RTCs in STMD processing not yet addressed.

AIM 2. **Nonlinear Facilitation for Long-Range Spatiotemporal Correlation in STMDs:** This goal was to determine experimentally if STMDs exploit the longer-range spatiotemporal correlations that arise due to the constraint that target motion occurs along continuous paths, and to elucidate the nature of the computations by which this is achieved.

AIM 3. **Further Characterization of STMD Behavior:** The goals included determination of the mechanism of the immense amplification required to support vigorous responses to sub-pixel targets; how inhibitory responses within the receptive field, or on earlier pathways to the STMDs, suppress responses to other features; and the range of 'non-target' stimuli (e.g. features of the background image) that produce responses from the STMD. To some extent, this goal was usurped by new findings that our experiments were recruiting a selective attention mechanism (see AIM 6 below)

AIM 4. **Improved 'Standard' Front End for Modeling:** The goal was to determine to what degree, and how, photoreceptor properties increase target detectability, to enable improved modeling of target detection.

AIM 5. **Improved Model for Wide-Field STMDs:** The goal was to develop a more capable wide-field STMD model that incorporates the spatiotemporal filtering characteristics of early vision, followed by rectification and adaptation inherent in the RTC, and a final stage based on a temporal nonlinear facilitation mechanism. One benchmark for this model will be to explain target motion detection without relative motion cues.

New Aims (as proposed in July 2012):
2 new aims (proposed in our July 2012 report) built on important new experimental physiological results obtained during the earlier part of this grant:

AIM 6. **Selective Attention in STMD neurons:** A key approach used of the earlier reporting periods for this project to address AIM 3 were experiments that involved the use of two targets, at variable locations within the receptive field, to characterize inhibitory interactions operating on different spatial baselines. These inhibitory interactions tune selectivity for

small features and assist rejection of background features. We published results addressing this aim during the first 3 performance periods, but several features of these data sets remained difficult to explain in large field STMDs such as dragonfly CSTMD1 neurons. In our more recent experiments we tested the hypothesis that the unexplained variation in our data results from the 2-target experiment paradigm itself recruiting a selective attention mechanism. The results obtained during the last part of this grant strongly support such a mechanism.

AIM 7. **Nonlinear spatiotemporal correlation between OFF and ON edges:** In our paper describing an initial model for the STMD (Weiderman et al 2008), we accepted the emerging view that early visual processing in insects segregates responses into ON and OFF channels, and postulated a mechanism for small target sensitivity that involves a supra-linear interaction between OFF channel response (as induced by leading edge of a dark target) and ON channel response (as induced by the trailing edge). (In particular, this mechanism accounts for sensitivity to smallness of the target in the direction of travel.) Direct evidence for this interaction was lacking, however, so obtaining such evidence and incorporating it into revised ESTMD model models formed the basis for the final aim addressed during the last 12 months of this project.

Status of the major project aims

Aims 1, 4 and 5 of the original grants were largely addressed by work reported in early progress reports and documented in our final report for FA9550-09-1-0116 (10 March 2012). In the final performance periods for FA2386-10-1-4114 (which ended up extended well beyond the original proposed schedule) we were able to make substantial progress towards addressing both aims 2 and 3, but our main effort was devoted to the new aims (6 & 7):

- **Aim 6.** At the conclusion of this project, we had also made substantial progress towards addressing aim 6. Initial results were described in our interim report (July 2012). A first paper was subsequently accepted for publication in the prestigious journal *Current Biology* (Wiederman & O'Carroll 2013a, published online December 2012). Our most recent work addressing this new aim offers the potential for a major future expansion of this project to use insect STMD neurons as an important new physiological model for understanding mechanisms of competitive selection and attention in response to multiple distractor features. Such a follow-on effort is supported from early 2013 by the award of a new 3-year project grant from the Australian Research Council.

- **Aim 7:** We have now tested this hypothesis in experiments where a target (with both leading and trailing edges) is drifted across the receptive field of the neuron and responses compared with those to a leading 'OFF' edge (an 'extending' dark bar entering the display), or a trailing 'ON' edge (a dark bar exiting the display) alone. We have further addressed this aim by elaboration of computational models that capture a number of key elements of the behavior of biological STMDs, including those arising from our earlier work on Aims 1-5.

3. Experiment:

The experiments described below focus primarily on the new work addressing aim 7, building substantially on the pilot data included in the interim report for FA2386-10-1-4114 (July 2012) and our final report for FA9550-09-1-0116 (10 March 2012). This experiment work was largely carried out by A/Prof O'Carroll and supported research fellow Dr Steven Wiederman using electrophysiological recording facilities methods and associated computational modeling in the Adelaide laboratory. This work was recently re-submitted to the prestigious Journal of Neuroscience (figures 1-7). The additional modeling documented here was (Figures 8-12) was recently submitted to the *2013 IEEE Symposium on Computational Intelligence for Multimedia, Signal and Vision Processing (CIMSIVP)*.

3.1 Nonlinear spatiotemporal correlation between OFF and ON edges:

Physiological recording: We inserted aluminium silicate glass microelectrodes (filled with 2M KCl,

80-120 MΩ) into the brain of immobilized *Hemicordulia tau* (n=13, either sex). We recorded intracellularly from individual neurons, identifying STMDs from their size tuning and characteristic receptive field, mapped using 37 horizontal and 21 vertical scans of a 1.25° dark target across a 120 Hz HD LCD monitor (100°x80° viewing extent) at 45°/s. For full details of these methods, see Bolzon et al., 2009. To study selectivity for dark targets, we drifted 1.25°x1.25° targets of varying luminance relative to the background at 45°/s horizontally through the strongest region of the receptive field. Nominal Weber contrasts were calculated from RGB values (linearized monitor, white background 315 Cdm^{-2}), C = (Target – Background) / Background.

ESTMD model: We implemented a model for an ESTMD in MATLAB as described in detail in Wiederman et al. (2008; 2009; 2010). This model accounts for the size and velocity tuning observed in insect STMDs and is robust in the presence of background clutter, even without relative motion cues (Wiederman et al., 2008), as observed in physiological responses of STMDs (Nordström et al., 2006, Wiederman et al., 2011). Parameters are based on fly physiology, with modification to match velocity tuning of the dragonfly (Geurten et al., 2007). Briefly, 2-dimensional spatial input is optically blurred (FWHM 1.4°) and hexagonally sampled (1° inter-receptor angle) at each time step (1KHz). Photoreceptor dynamics are based on the model proposed by van Hateren and Snippe (2001). Spatial antagonism of the 1st order interneurons (LMCs) was implemented via weighted subtraction of nearest neighbours in the hexagonally sampled inputs to allow transmission of 70% static luminance and thus match the weak lateral inhibition described from LMC recordings in the same dragonfly species (Laughlin, 1974). LMC temporal filters were derived from Juusola et al. (1995) implemented with a relaxed high-pass filter (lower corner frequency 8 Hz) and a small DC component (10%).

The LMC output was fed into an additional stage which took direct inspiration from our electrophysiological recordings from rectifying transient cells (RTCs, see AIM 1) described from the locust medulla (Osorio, 1991, O'Carroll et al., 1992), and 1st optic chiasm and the medulla of the blowfly (Jansonius and van Hateren, 1991, Wiederman et al., 2008). In these RTCs, transient ON and OFF phases (from the LMC high-pass filtering) are separated via a further temporal high pass filter (τ = 100 ms or 200 ms) to remove any sustained signal component before half-wave rectification with each channel exhibiting independent and fast adaptation. Adaptation states for this stage are determined by a nonlinear filter which approximates cellular 'fast depolarization and slow repolarization' responses, which switches its time constant dependent on whether the input is increasing or decreasing ('fast', τ = 3 ms, when channel input is increasing and 'slow', τ = 70 ms, when decreasing). A key property that results from inclusion of this complex, nonlinear filtering is the selectivity for 'novel' transient contrast changes, with the suppression of fluctuating textural variations. This temporal processing thus explains the robustness of STMD neurons to contrasting targets against complex backgrounds.

The next model stage includes strong surround antagonism with ON channels inhibiting ON and OFF inhibiting OFF, as clearly observed in blowfly RTCs (Jansonius and van Hateren, 1993). This 'like' channel inhibition is essential to suppress responses for features that are extended along the axis orthogonal to their motion (i.e. the 'hypercomplex property' - selectivity for small objects versus extended bar features, Nordström & O'Carroll 2009). The RTC output then combines ON and OFF channels via a facilitatory interaction between the delayed OFF channel (low pass filter, τ = 25 ms) and the undelayed ON channel. This is modeled with a multiplication operation; for generality, linear terms may also be included: a•[ON] + b•[$OFF_{delayed}$] + c•[ON]•[$OFF_{delayed}$].

Comparison of ESTMD and EMD models: For comparison with the ESTMD, EMD models were implemented using the basic schemes described for a 2-detector EMD by Eichner et al. (2011) and a 6-detector EMD by Clark et al. (2011) except that these were implemented using the same optical blur, hexagonal sampling, inter-receptor angle, and early visual filtering as the ESTMD described above (i.e. photoreceptor and LMC stages). The signal was then half-wave rectified into ON and OFF channels. The 2-detector EMD model sums the output of individual correlations between ON with ON ('L1 pathway', Fig. 1B) and OFF with OFF ('L2 pathway') channels. The 6-detector model (Fig. 1C) includes additional correlations between opposite signs of contrast polarity (weighted as in Clark et al. 2011), i.e. correlations between ON with OFF channels as well as between OFF with ON

channels. Both EMD and ESTMD models were implemented as a hexagonal grid of local detectors spanning an 80°x80° field. Data in Figure 6 were from a single ESTMD within this grid, centred on the target trajectory. Data in Figure 7 were summed over the entire array to mimic the output of a higher-order lobula plate tangential neuron and allow us to measure responses where the leading and trailing edges of the bar stimuli may be widely separated.

4. Results and Discussion:

4.1 Separation of OFF and ON pathways in insect vision

The dominant computational model for biological motion processing for 50 years, the Hassenstein-Reichardt (HR) model for an elementary motion detector (EMD), involves correlation of spatially separated contrast signals after delaying one channel (Fig. 1A). This model is supported by diverse evidence from behavioural and electrophysiological studies, particularly in dipteran flies (Hassenstein and Reichardt, 1956, review Borst and Euler, 2011), but its specific neural implementation remains elusive. In particular, the degree to which contrast signals are separated into parallel ON and OFF pathways (for luminance increments and decrements) and then recombined within the EMD has been questioned for many years (Egelhaaf and Borst, 1985; Franceschini et al., 1989). Data from downstream Vertical and Horizontal System neurons used for optic flow analysis by dipteran flies supports a 2-detector EMD (Fig. 1B) in which ON-ON and OFF-OFF information is correlated locally in parallel pathways which are then summed (Eichner et al., 2011, Joesch et al. 2013).

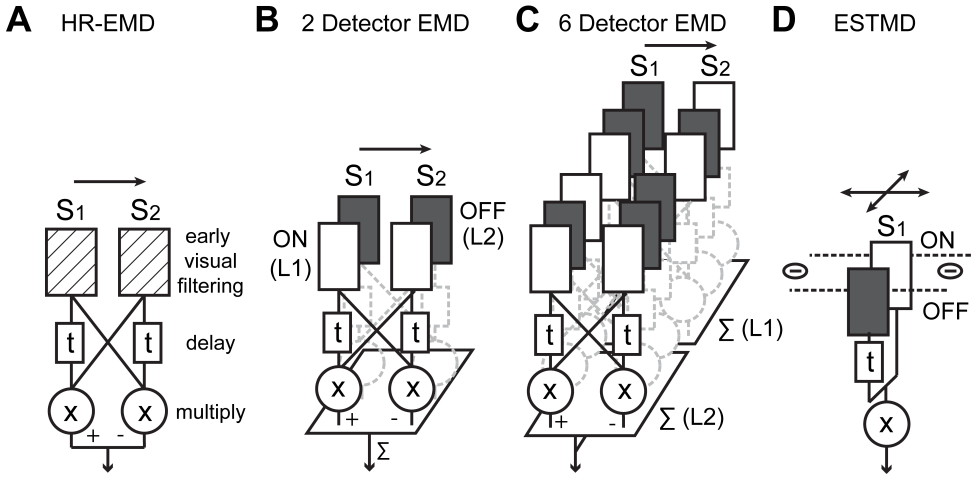

Figure 1. Correlation based models of elementary motion detection. ***A***, The Hassenstein-Reichardt EMD correlates spatially separated luminance signals (S_1 and S_2) with one path delayed in time. The subtraction of a mirror symmetric unit provides opponent direction selectivity to the EMD. ***B***, In the 2-detector EMD (Eichner et al., 2011), like channels are correlated with one another, i.e. ON with ON (L1) and OFF with OFF (L2). L1 and L2 refer to types of laminar monopolar cell. ***C***, The 6-detector EMD (Clark et al., 2011) has more complex combinatorial interactions between channels, including correlation between spatially separated OFF and ON signals. ***D***, In the ESTMD model, center-surround antagonism of ON and OFF channels is followed by the correlation of the delayed OFF with the undelayed ON signal.

Insect small target motion detector (STMD) neurons have been characterized in the lobula and lateral midbrain of both dragonflies (O'Carroll, 1993, Geurten et al., 2007) and dipteran flies (Nordström et al., 2006; Nordström and O'Carroll, 2006; 2009, Barnett et al., 2007). Typical STMDs respond robustly to small moving targets (subtending ~1-3°) even against background clutter (Nordström et al., 2006; Wiederman and O'Carroll, 2011). In an attempt to explain these properties, we previously proposed a model for an elementary small target motion detector (ESTMD)

employing a correlation of ON signals at each location with delayed OFF to match the expected signature of a small, dark feature (Fig. 1D):

Despite the ESTMD model providing an excellent fit to the spatiotemporal tuning of STMD neurons, several key predictions of it remain untested. Our experiments in the final phase of this grant aimed to address this deficiency via recordings both from CSTMD1 and from several other types of dragonfly STMD. We obtained evidence for a potent non-linear interaction between OFF and ON channels in this alternative motion pathway. We show that many STMD neurons only respond to dark objects, with little or no response to light objects with equal contrast. These responses are greater than predicted from the linear combination of responses to dark or light edges of identical, limited lateral extent. Finally, we show that classical HR-EMD models (either with or without strong surround antagonism) cannot account for our data, but our model of STMD neurons is well matched (Wiederman et al., 2008; 2010). Thus we provide evidence that feature-specific information is extracted by operations involving the supralinear combination of ON and OFF contrast pathways in the dragonfly brain.

ESTMD model

Although variants of the HR model (Fig. 1A) have previously been used to model spatiotemporal tuning of STMD neurons (Geurten et al., 2007, Dunbier et al., 2011; 2012), these models lack the size selectivity that characterizes STMDs. We therefore previously proposed the ESTMD (Fig. 1D) as a model for a fundamental, local signal processing stage underlying STMD behavior (Wiederman et al., 2008; 2009), which is then summed spatially by wider-field STMD neurons amenable to electrophysiological study.

Like the 2-detector EMD proposed by Eichner et al. (2011) (Fig. 1B), our ESTMD model incorporates separation of half-wave rectified ON and OFF channels. In *Drosophila*, behavioral responses provide evidence for additional OFF-ON and ON-OFF interactions (Fig. 1C) that characterize a more complex 6-detector EMD model (Clark et al., 2011). Unlike the 2-detector EMD, but as in two subunits of the 6-detector model, the ESTMD involves correlation of opposite sign channels (Fig. 1D). Unlike any variant of the EMD proposed to date, however, the ESTMD correlates ON with delayed OFF signals arising at the *same* retinotopic location, rather than from adjacent or nearby detector pairs. This exploits properties of a spatially circumscribed feature moving in a given direction: even against cluttered backgrounds such a feature is likely to have a leading edge luminance change opposite in sign to its trailing edge. A tiny dark object crossing the receptive field of a single photoreceptor would thus produce a response that first falls before rising.

The addition of strong surround antagonism within the ESTMD further enhances small target selectivity along the axis orthogonal to its motion, while rapid adaptation in the rectifying ON/OFF elements rejects repetitive local flicker stimuli induced by background texture. Although STMD neurons show varying degrees of direction selectivity (O'Carroll 1993, Nordström et al. 2006, Barnett et al. 2007) the ESTMD model as originally formulated (Wiederman et al., 2008) is inherently non-directional. The inclusion of direction selectivity in the ESTMD, however, can be readily modeled by several alternative mechanisms without changing the fundamental selectivity for small features (Wiederman & O'Carroll 2013a). These include spatial separation of the correlated ON and OFF channels, asymmetry in the inhibitory surround, or 2nd order ESTMD-like correlation of inputs derived from 2-detector EMDs (or vice versa).

Selectivity for dark features

An untested prediction arising from the opposite-polarity correlation in the ESTMD model is its selectivity for the sign of the contrast 'signature' produced by a given target. The detection of both light and dark targets would require local ESTMD pairs to correlate both delayed ON with OFF, and delayed OFF with ON channels, while a simpler ESTMD (as in Figure 1D) would be selective for dark features. To test whether this is the case, we quantified contrast sensitivity of 10 feature-detecting neurons by drifting small light (i.e. an ON-OFF stimulus) or dark (OFF-ON) targets through the receptive field. We presented different combinations of stimuli comprising 'OFF' and 'ON' edges, as well as 'Target' features. Figure 2 describes these stimuli in detail. In each panel, the upper pictograms describe the stimuli at a single point in time (i.e. a diagrammatic 'snapshot' of our

stimulus screen). The lower panel shows a space/time plot of the corresponding stimulus, i.e. the luminance change along the line that the feature moves along. Each stimulus had identical, limited spatial extent (1.25°) in the axis orthogonal to its motion. These were each presented at 4 different locations within the ~80° degree wide receptive field of CSTMD1 (at 5° separations). We included a minimum rest interval of 50 seconds between stimuli presented at the same receptive field location. This was aimed at minimizing local habituation effects. Edges and targets were presented at high contrast (Fig. 2A), low contrast (Fig. 2B) and at both contrast polarities (Fig. 2C).

In 6 recordings from the identified neuron, CSTMD1 (Fig. 3A) and 4 from unidentified STMDs (Fig 3B) we observed profound dark target selectivity. Figure 3A shows mean spike rate for an example CSTMD1 neuron (within a 500ms analysis window centered on the receptive field) in response to a range of target contrasts of both light and dark polarities (mean ± SEM of 5 trials). As targets get darker, spike rate increases. However responses to light targets elicit minimal response even at the highest contrast. Data averaged across 5 CSTMD1 neurons (Fig. 3A, inset) confirmed selectivity for the polarity of the stimulus, with a significantly larger response to dark (C_{Weber} = -1) versus light (C_{Weber} = 1) targets (P=0.009, paired t-test). Indeed, responses to light targets are not significantly above spontaneous levels.

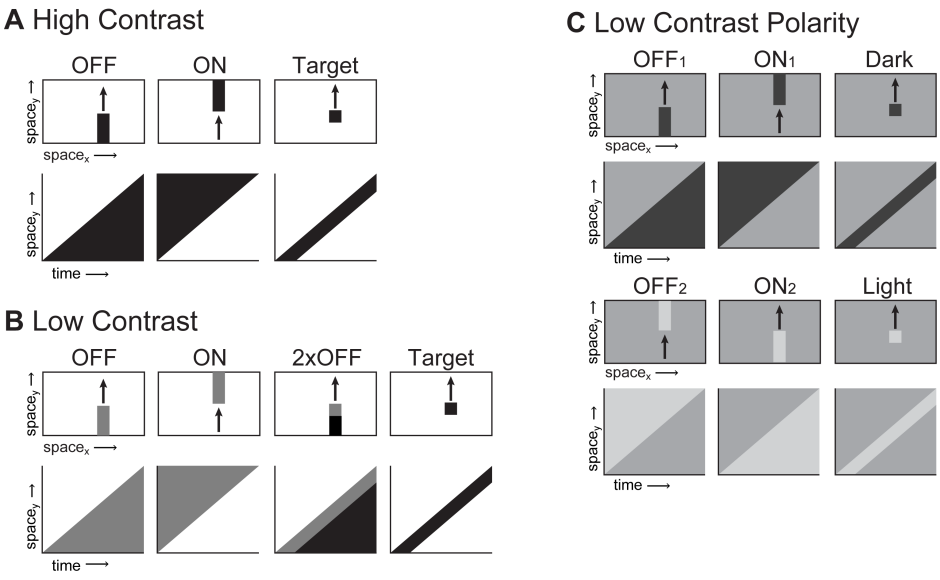

Figure 2. Visual stimuli presented to the dragonfly during electrophysiological recordings from STMD neurons. Upper rows of each combination depict a snapshot in time of the 2-d display on which stimuli were presented (not to scale) while lower rows are space-time plots for the luminance change along the line that the feature moves. ***A,*** High contrast OFF and ON edges and a single black target are drifted from the bottom to the top of the display. ***B,*** Low contrast versions of both edges and target, with the addition of a 'target' composed of two OFF edges. ***C,*** On a mean background, ON and OFF edges are composed from both mean background to light and mean background to dark transitions. Both light and dark targets are also presented.

The four unidentified feature-selective neurons (Fig. 3B) all show varying degrees of size selectivity for targets or short bars (determined from size-tuning, Fig. 3B, inset) between 1 and 10° (i.e. orthogonal to the direction of travel). In all of these feature-selective neurons, darker targets evoked robust responses saturating at relatively low contrasts (C_{Weber} between -0.2 and -0.5). They all elict very weak responses to high contrast light targets (Fig. 3B), thus confirming that dark target selectivity is not unique to CSTMD1. If we present light targets against a black screen background (a stimulus that represents a much higher Weber contrast) we do see intermittent weak responses

(data not shown). We excluded this data from our quantitative analysis, however, because it subjects the photoreceptors to a significantly lower adapting luminance, well below the physiologically normal range.

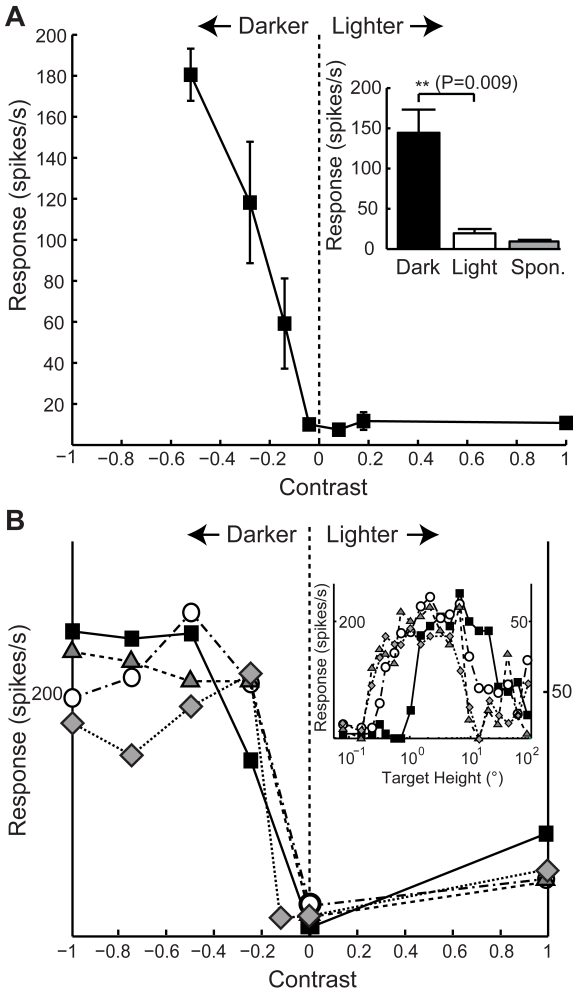

Figure 3. Dark target selectivity in the dragonfly brain. ***A***, An individual example of CSTMD1 responses to targets of varying contrast moving on a mid-luminance background (mean±SEM, 5 trials). Responses strengthen as negative contrast polarity of the target increases (dark), however positive contrast (light) targets elicit little response. Across 5 neurons (inset graph, mean ± SEM), CSTMD1 displays dark target selectivity, responding significantly more (P=0.009) to high contrast black targets (C_{Weber} = -1) than to high contrast white targets (C_{Weber} = 1), which are indistinguishable from spontaneous activity. ***B***, Four unidentified neurons in *Hemicordulia tau* produce robust responses to targets of increasing dark contrast but not to light contrast (left ordinate: black squares and grey diamonds; right ordinate: grey triangles and white circles). These unidentified feature-selective neurons exhibit varying size-selectivity (inset graph).

Supralinear summation of edge responses

From Figure 3, we conclude that STMD neurons show dark target selectivity consistent with predictions of an ESTMD model that correlates delayed OFF with ON information. To further test whether this involves a supralinear interaction between these channels, we presented STMD neurons with moving ON and OFF features with limited extent in the dimension orthogonal to their motion (i.e. local edge features) and compared responses with those for the equivalent discrete

targets. These stimuli are illustrated by the pictograms in Figures 2 and 4. Figure 4A shows mean peristimulus time histograms from two individual CSTMD1s in response to the different stimuli. In the first example, we repeated each stimulus 5 times at 4 locations within the receptive field (20 trials). Both OFF edge (dashed line) and ON edge (dotted line) responses are weak. Target responses (solid line) are greater than the linear combination of the ON and OFF edge responses. In a second CSTMD1 example (16 trials), OFF edges produce moderate responses that are stronger than ON edge responses. Figure 4B shows the responses to the same stimuli for one of the unidentified neurons (STMD-U1), which also resulted in a supralinear target response.

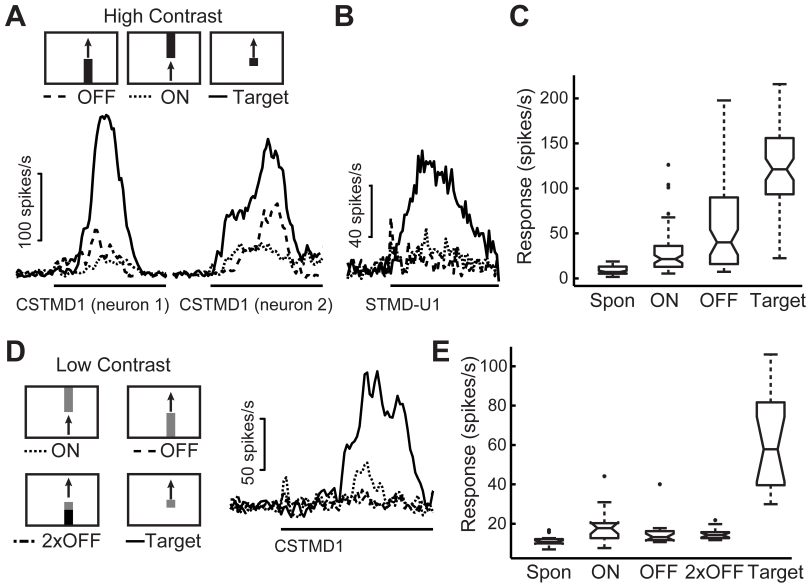

Figure 4. ***A***, Two examples of individual CSTMD1 responses to high contrast stimuli drifted through the receptive field. In the first, CSTMD1 exhibits little response to either ON or OFF edges and the response to targets is larger than a linear combination of the edge responses (mean of 20 trials). In the second example, CSTMD1 responds to high contrast ON and OFF edges, though both are weaker than target responses (mean of 16 trials). ***B***, The response of an un-identified STMD neuron to the same stimuli exhibits a similar supralinearity (mean of 20 trials). ***C***, Pooled CSTMD1 responses (68 trials over 5 neurons) show median target responses are larger than the linear combination of responses to ON and OFF edges (Target vs. ON + OFF, P = 0.001, Mann-Whitney U). In some trials, edge responses evoke responses from CSTMD1 in particularly to the OFF stimulus. ***D***, CSTMD1 responses to lower contrast target and edges stimuli (C_{Weber} = -0.6) and a 'double' OFF edge stimulus (white to grey to black). An example CSTMD1 response to the lower contrast stimuli exhibits strong target responses and weak response to either ON or OFF edges. Furthermore, the double OFF/OFF stimulus elicits minimal response (average of 12). ***E,*** CSTMD1 target responses are greater than any linear combination of the ON and OFF edge responses (16 trials over 2 neurons).

To examine reproducibility of responses in CSTMD1, we pooled results from 5 neurons (Fig. 4C, 1s analysis window, 68 trials). There is a significant difference between all 4 conditions: $P<0.05$ (ON vs. OFF), $P<0.001$ (others), Dunn's multiple comparison, Kruskal-Wallis. Furthermore, target responses are significantly higher than the sum of the ON and OFF edge responses (P = 0.001, Mann Whitney U), thus supporting a supralinear interaction between the OFF and ON channels.

With the high contrast stimuli in Figure 4A-C, many individual trials produce strong edge responses, particularly to the OFF stimulus, and target responses may easily exceed 300 spike/s. We briefly discussed this variation in our previous progress report (July 2012) for this project and speculated as to possible causes. In particular, saturation could potentially mask the full degree of the

non-linear interaction between OFF and ON channels. We therefore also presented lower contrast versions of the stimuli (see Fig. 2B) to 2 CSTMD1 neurons (16 trials total). This allowed us to also test a further variant, a 'double' OFF-edge stimulus (also mentioned in the previous report). This comprised a white to grey transition on the leading edge of the feature, followed by a further grey to black transition, separated by 1.25° (Fig. 2B). This feature induces luminance changes similar in contrast and spatial extent to the low contrast dark target, except that the polarity of the trailing edge is the same as the leading edge.

Figure 4D shows mean responses to these stimuli in an example CSTMD1, revealing potent supralinearity of the target response relative to ON and OFF edge responses. When pooled over the entire set of 16 trials (Fig. 4E), the mean target responses are much larger than for any of the other conditions, including the double OFF-edge stimulus. This suggests that the target response requires ***both*** ON and OFF channels.

In order to test stimuli for both light and dark contrast edge polarities we also presented low contrast stimuli against a mean luminance (grey) background (Fig. 2C) in two further CSTMD1 neurons (Fig. 5A, 12 trials). Dark target selectivity is again evidenced by the much stronger response to dark targets than any other combination of light or dark contrasting edges. Some of the variation evident in the box-plot distributions in Figure 5A is due to the inhomogeneous sensitivity at different locations within the receptive field over which stimuli were presented. Figure 5B shows individual responses to low contrast dark targets plotted against the sum of the OFF and ON edge responses matched to the same location in the receptive field. Observed responses to low contrast dark targets are clearly always much stronger (dashed line, slope = 1.9±0.4 [95%CI]) than the predictions of the linear sum of ON and OFF responses (solid line, slope=1).

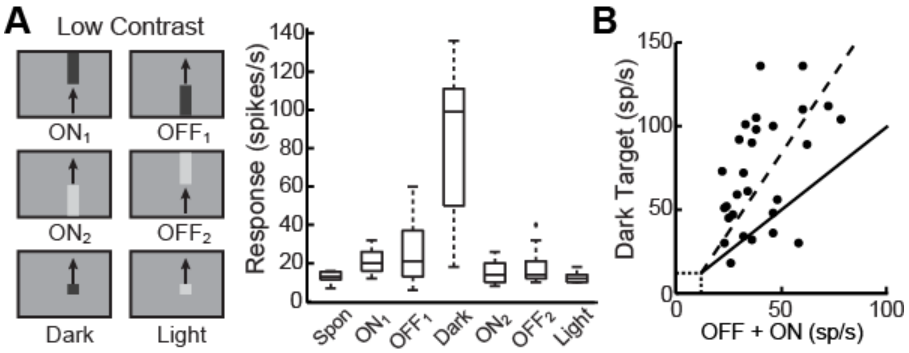

Figure 5. CSTMD1 responses to low contrast edge and target stimuli ***A,*** Irrespective of the edge transition with respect to the background (i.e. ON_1: dark to mean or ON_2: mean to light; OFF_1: mean to dark or OFF_2: light to mean), CSTMD1 responses in a further 2 neurons (12 trials total) are much stronger to the dark target. These dark target responses are much larger than those to the light target or the linear combination of either of the ON and OFF edge combinations. ***B,*** CSTMD1 responses to low contrast dark targets are plotted against the linear sum of ON and OFF responses (matched at the same receptive field location). Solid line represents a linear combination (slope of 1), dashed line of best fit (slope = 1.9±0.4 [95%CI]).

Evidence for an ESTMD-like mechanism

Taken together, our experimental data confirm that:

(1) Only dark targets evoke robust spiking activity from CSTMD1,
(2) The target response involves a potent supralinear interaction between nearby edges.
(3) The target response requires both OFF and ON components.

Can we reproduce these results with the ESTMD model that we previously proposed (Wiederman et

al., 2008)? Figure 6 shows data for ESTMD models that include ON and OFF channels that interact both linearly and multiplicatively: a•[ON] + b•[$OFF_{delayed}$] + c•[ON]•[$OFF_{delayed}$]. The data show distributions for outputs of our model in response to similar stimuli to those presented to STMD neurons in Figures 4 and 5 (i.e. at both high and low contrast) and using combinations of coefficients *a,b* and *c* varied over a large range: *a* {0, 1, 2}; *b* {0, 1, 2}; and *c* {1, 2, 5}. These combinations of term coefficients allow us to represent different 'balances' of interactions between separate ON and OFF channels.

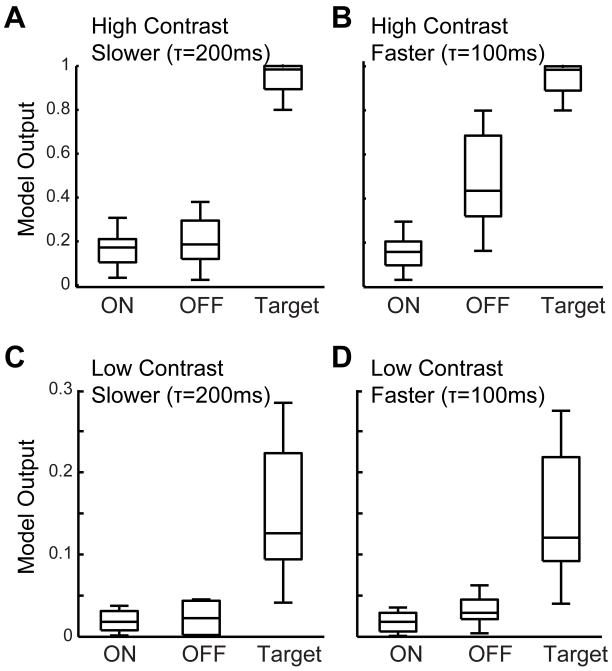

Figure 6. An ESTMD model includes terms for separate ON and OFF channels, as well as a facilitatory correlation between the delayed OFF and undelayed ON signals. a•[ON] + b•[$OFF_{delayed}$] + c•[ON]•[$OFF_{delayed}$]. We varied *a*, *b* and *c* coefficients and examine their pooled effect on each distribution of ON edge, OFF edge and target responses. All model variants predict supralinear target responses, ***A***, High contrast stimuli and more sustaining high pass filtering (τ=200ms), predicts either or both ON and OFF edge responses. ***B***, High contrast and more transient high pass filtering (τ=100ms) produces larger OFF edge responses, as observed in experiments (Fig. 6B cf. Fig. 4C). ***C***, For lower contrast stimuli the ESTMD model predicts minimal ON or OFF edge responses, again matching the physiological data (Fig. 6C,D cf. Fig. 4E,5A).

As can be seen from Figure 6, the ESTMD model captures not only the supra-linear interaction between the ON and OFF components of the target stimulus, it also predicts the presence of weak responses to the ON and particularly the OFF edges at high contrasts (Fig. 6A,B), as we observed in the STMD recordings (Fig. 4,5). This is, perhaps, surprising given that the distributions include combinations of term coefficients where a=b=0, i.e. a purely multiplicative ESTMD. However, with appropriate temporal high pass filtering in early vision, a single edge stimulus can potentially induce excitation of both ON and OFF channels due to response rebound following the initial luminance change. Even in the photoreceptors themselves, luminance step responses may show complex multiphasic transients at high contrasts even though they encode luminance steps faithfully at low contrasts (Laughlin and Weckström, 1993). Such complex temporal filtering would lead to weak outputs from even a purely multiplicative ESTMD. In addition to varying the term coefficients, we further tested 2 model variants (τ=200ms, τ=100ms) that simulate variation in high pass filtering that could represent differences in the state of light adaptation (van Hateren and Snippe, 2001; Juusola et al., 1995) or even a change in temperature (Tatler et al., 2000). At low contrasts (Fig. 6 C,D) the model is relatively robust against the differing contributions of the term coefficients within the range we considered, and always shows the strongly supralinear interaction effect as seen in the

physiological data (Fig. 4, 5). The faster time constant model better matches the physiological data, however, in that it gives stronger responses to dark edges at high but not lower contrast (compare Fig. 6B,D with Fig. 4C,E).

Comparison with EMD models

From Figure 6 we conclude that with careful attention to the temporal properties of high-pass filters that are a key element of the model, an ESTMD-like mechanism can explain selectivity for dark features and the supralinear interaction between nearby ON and OFF edges that we observe in STMD neurons. Given that it also includes a multiplicative interaction, could a simple Hassenstein-Reichardt correlation EMD be an alternative explanation for our data?

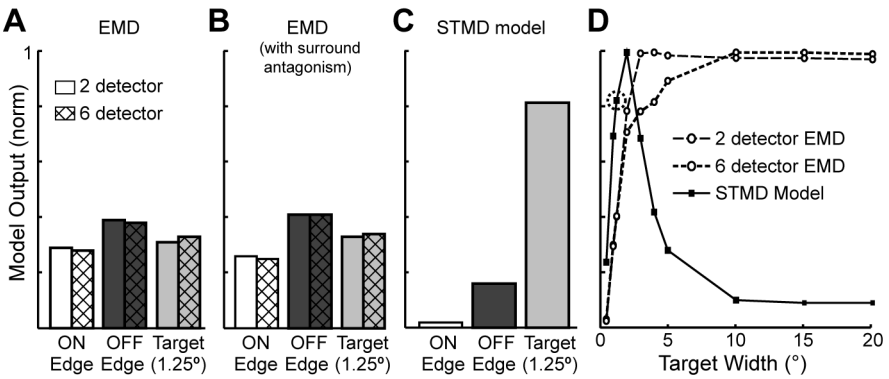

Figure 7. Edges (ON & OFF) and dark targets serve as input to model variants of the EMD as well as the ESTMD model. These include both the 2-detector EMD, which sums channels of 'like' correlations (Eichner et al., 2011) and the 6-detector EMD, which includes terms between ON and OFF correlations (Clark et al., 2011). Each of these versions are modeled with and without strong surround antagonism. For each model variant, output is normalized to the sum of the OFF edge, ON edge and target output values. ***A,*** Without surround antagonism both the 2 and 6-detector models predict a sublinear response to targets rather than the supralinearity observed in CSTMD1 (Fig.4C, E and Fig. 5). ***B,*** Model outputs do not change when surround antagonism is included in the model variants. ***C,*** In comparison, an STMD model matches the physiological data with target responses much larger than the linear combination of ON and OFF edge responses. ***D,*** EMD and STMD model output in response to targets of varying extent (in the direction of travel). The ESTMD model is more responsive to small targets and the output of the OFF and ON correlation is inherently tuned to the separation of the OFF and ON edges in the direction of travel (i.e. velocity/width tuned).

On the contrary, corresponding models for both a 2 and 6-detector EMD yield sublinear addition of the single edge responses compared with the response to the tiny targets used in our experiments (Fig. 7A,B). This is in contrast to the output supralinearity observed in our ESTMD model (Fig. 7C). This is because optical blur by the facet lenses (Horridge, 1978, Nordström et al., 2006) has a greater effect on the small targets compared with the single-edge stimuli, which are blurred only across their narrow dimension. Therefore, in comparison to the moving edges, target responses are expected to be *weaker* at the earliest stages of visual processing despite the inclusion of a front-end for all 3 model variants including processing that accounts well for both linear and non-linear spatiotemporal filtering in early visual processing (Laughlin 1974, van Hateren & Snippe 2001, Brinkworth et al. 2008, Mah et al. 2008, Wiederman et al. 2010). This makes the observed strength of the response to the target versus single edges in the STMD recordings all the more impressive.

Arguably, the contrast attenuation of small features could be partially offset by the strong surround antagonism that represents an additional stage of the ESTMD model. We tested this by simulation of additional variants of the 2 and 6-detector EMD models that include this extra stage of processing (Fig. 7B). Again target responses are weaker than the linear combination of the single edge responses. If we extend the target width in the direction of travel (Fig. 7D), optical blur has less

effect on the target, which begins to resemble a double edge stimulus (i.e. an OFF leading edge widely separated from an ON trailing edge). With two edge features within the scene, both EMD variants tested then yield responses greater than ON or OFF edge stimuli alone, but never exceed the linear combination of ON and OFF edge responses (Fig. 7D). The ESTMD, by comparison, responds progressively more weakly (as observed in STMD neurons) as the leading and trailing edge become further separated in time.

4.2 Velocity tuning and contrast polarity

STMDs are tuned to the velocity of a moving target. This property is itself indicative of an underlying mechanism that likely involves some form of spatio-temporal correlation (Geurten et al. 2009; Nordström and O'Carroll, 2006). Although we previously suggested this provides evidence for an HR-EMD framework, the result is equally consistent with the ESTMD-based correlation model. In any such model, a pronounced velocity optimum is determined by early visual filtering and the correlation delay time constant (Geurten et al., 2009; Dunbier et al., 2012), with the optimum velocity increasing as target width increases in the direction of travel (Geurten et al., 2009). This is due to the increased spatial separation between the leading and trailing edge of the target, requiring a faster transit speed to match a given delay between OFF and ON channels. The ESTMD, as a 'temporal' correlator, can extract this weak rising and falling signature of a target even though it primarily occurs in a single ommatidium at a time. Although directionality may be readily explained with the inclusion of spatial interactions or asymmetry (Wiederman and O'Carroll, 2013a), a benefit of (purely local) temporal processing is the robust responses to slowly moving targets smaller than a single ommatidium – a simple form of hyperacuity. In fact, many STMD neurons (including CSTMD1) are responsive to target sizes of less than 0.5° square, which are of extremely low effective contrast (*Eristalis tenax*, Nordström et al., 2006; *Hemicordulia tau*, Wiederman & O'Carroll 2013b).

Our modeling shows that the pattern of responses observed in STMD neurons to single edge versus target features is poorly predicted by HR-EMDs, but well predicted by an ESTMD mechanism. A side effect of the very high gain required to achieve the observed sensitivity for the blurred image of very small targets is some sensitivity to high contrast edges with limited angular extent. Natural scenes, however, are dominated by larger features (Dror et al., 2000) and our own recording from STMDs in response to natural scenes shows that breakthrough responses from textural features of the background are weak even in strong clutter (Wiederman & O'Carroll, 2011). To account for some ON and OFF edge excitation, we include linear terms in our phenomenological model. What would the three terms of our model represent physiologically? They suggest a mechanism of interaction that involves weak excitation by the individual signals that impinge on the individual arms of the correlator, with significant enhancement of excitation by their co-activation. Significant variation in single-edge sensitivity seen in CSTMD1 from animal to animal could reflect varying excitation thresholds or variation in the strengths of the individual inputs relative to their degree of mutual facilitation.

Hawking dragonflies, such as *Hemicordulia tau*, remain continuously in flight, swooping upwards to catch their prey overhead (Corbet, 1999). In this scenario, the target prey is located within an area of high visual acuity (Horrige, 1978) and will appear dark against a light sky background. However, we also observe dragonflies chasing prey and conspecifics against cluttered surrounds, with the changing background causing the perceived target to alternate between light and dark contrasts. From the behavioral perspective, it would seem that neurons responsive to either or both light and dark targets should exist. Our encountering of only dark target selective neurons to date may be coincidental or possibly the result of bias in our experimental preparation, which is geared towards recording neurons with dorsally-centered receptive fields. From the modeling perspective, should light-target selectivity be observed in future, this problem is readily solved with the inclusion of an $[ON_{delayed}]$•[OFF] term to form a light-target-sensitive ESTMD.

Although we present results from several types of STMD neurons, our primary evidence is derived from recordings of CSTMD1. This neuron has visual inputs in the mid-brain and has recently been shown to exhibit several 'higher-order' attributes. These include the ability to selectively attend to a single target in the presence of a distractor (Wiederman and O'Carroll, 2013b), as well as exhibiting

a slow facilitation of its response for targets that move along a continuous trajectory (Nordström at al. 2011; Dunbier et al. 2012). However, CSTMD1 is a neuron that responds very quickly in absolute terms, with a response latency less than 50 ms (Nordström et al. 2011) and tuning to high target velocity (Geurten et al. 2007; Dunbier et al. 2012). Our modeling of its response kinetics suggests that the facilitation must be due to a higher order property within the STMD pathway (e.g. attentional modulation) in response to slower moving features, rather than any inherent sluggishness in the time constants of the underlying motion pathway (Dunbier et al. 2011; 2012). Thus, some caution is still in order in attributing the observed supralinear response characteristics of CSTMD1 to an underlying elementary correlation between local OFF and ON channels, versus a mechanism that up-regulates attention for the highly salient target stimulus. Nevertheless, the fact that we also observed similar supralinearity in several other unidentified STMD neurons, suggests that this is a common property of the input pathway.

4.3 SF-STMDs, Direction selectivity higher order facilitation: could a 2nd order detector provide a unified solution?

While our data above provides strong evidence for an ESTMD-like mechanism being involved in the STMD neuronal pathway, it falls short of explaining all observed properties of typical STMDs. In particular, while CSTMD1 itself is not direction-selective, other STMDs are. Indeed, successful tracking and interception of targets must involve additional information about both direction and location of the target. Secondly, the non-linear facilitation mechanism that we have described in detail in earlier reporting periods (and the associated papers) is not an emergent property of local ESTMD processing. It must result instead from interactions occurring over larger spatial baselines – i.e. between ESTMDs (or their output collators) themselves. An interesting hypothesis to explain both phenomena is that they employ a second-order motion detector that cascades an HR-type EMD stage with an ESTMD stage. This is further suggested by the our discovery of direction-selective STMD neurons with relatively small receptive fields, around 5-10° across (where the inter-detector angle of the insect is 1-1.5°) (Barnett et al 2007). While signaling local motion of small features, these small-field STMDs (SF-STMDs) still encapsulate inputs corresponding to a local pool of dozens of adjacent input ommatidia, so could easily represent the output of an asymmetric, non-linear integration of local ESTMDs – i.e. a 2nd order motion detector network.

Consistent with this notion, a 2nd order operation was recently proposed following our recent finding (reported in the early stages of the current project) that the response time-course in the large-field dragonfly STMD neuron CSTMD1 to small target stimuli builds to a maximum over several hundred milliseconds (Nordström et al 2010). It does so, however, only for targets that successively track across tens of degrees of visual angle, and thus large numbers of local ommatidia, as quantified in our earlier reporting periods. A second-order motion detector network might not only confer direction selectivity, but could potentially enhance target detection by taking advantage of a distinguishing characteristic feature of natural target motion: true targets tend to move along continuous paths, even if they change direction or vary in contrast as they move across the background. A response in one local motion detector should be well correlated with an appropriately delayed response in neighbouring detectors (i.e. matching the target velocity). Noise, on the other hand (including spurious feature motion of the background, such as foliage moving with wind), would be local and inconsistent, and thus less likely to persist along continuous trajectories. A second-order system would thus enhance rejection of feature motion not correlated across multiple local adjacent input detectors, permitting amplification to enhance robustness whilst maintaining underlying selectivity to stimuli on the spatial scale of single ommatidia of the eye.

To test this, we further developed several variants of computational models that capture the key properties of direction-selective SF-STMD neurons by cascading partially rectified ESTMD stages with HR-type EMDs, and vice versa. We then examined the key response tuning and predictions of these second order systems for simple stimuli. We developed three versions of the target-detection model each including identical 'biomimetic' front-end processing. These computational models simulated insect optics (blurring and hexagonal sampling) and early visual processing (dynamic bandpass filtering) as described in the Appendix. These 3 model variants comprised:

(1) The first variant was simply our ESTMD model as described (and applied) above (i.e. in Figure 1D). This includes strong surround antagonism and correlates a delayed OFF channel with an undelayed ON channel.
(2) A second variant 2nd order 'hybrid' EMD-ESTMD model (Figure 8A). This implements a front end based on a direction-selective 2-detector EMD (as in Fig. 1B) that separates ON and OFF channels and then subsequently correlates these 'like' channels in separate multiplication stages. This EMD is based on the recent findings from genetic modification of fruit-fly vision (Eichner et al., 2011, Joesch et al. 2013) and is currently regarded as the 'state of the art' as a biomimetic model for the HR-EMD as observed in insects. In our hybrid EMD-ESTMD model (Figure 8A) each 'ON-ON' and OFF-OFF *motion* signal at the output of the 2 EMDs then serves as input to a 2nd order ESTMD stage which correlates the delayed signal from the OFF EMD with the undelayed ON EMD.
(3) A third variant 2nd order hypdrid (ESTMD-EMD) variant (Figure 8B) implements these same operations in reverse order, i.e. the model first computes the 'matched target' filter with an ESTMD (as in Figure 1b), before correlating these as inputs to a 2nd order 2-detector EMD (as in Figure 1B).

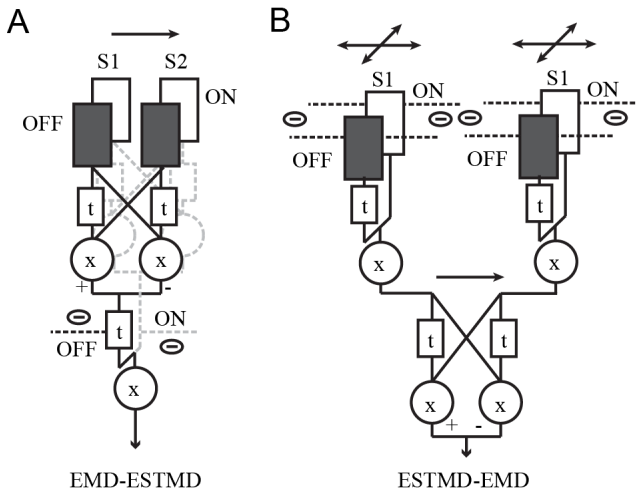

Figure 8: A. The cascaded EMD-ESTMD model uses spatiotemporally correlated ON and OFF channels to serve as inputs to an ESTMD model. B. The cascaded ESTMD-EMD model adds directionality to target detection by correlating the output of two non-directional ESTMD units.

Figure 9 shows that both hybrid models lead to a direction-selective output. The figure shows the percentage strength of directionality, defined here relative to the sum of the response to targets moving in in two opposite directions. The target stimulus subtended an angle of 1.25° x 2° and moved at a speed of 45°/s. As can be seen the ESTMD responds equally to either target direction and is in effect a local flicker detector, matched to the spatiotemporal profile of a moving target. By cascading a 2 detector EMD either before (EMD-ESTMD) or after (ESTMD-EMD) the matched filter induces strong directionality to the model responses, with responses in the 'preferred' direction comprising almost 100% of the overall response to both.

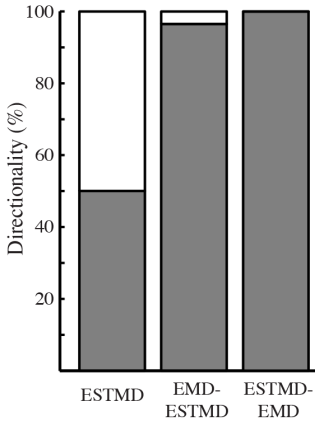

Figure 9: Results showing that the ESTMD model responds equally to target motion in either direction (1.25° x 2° at 45°/s), while addition of a 2 detector EMD cascaded either before (EMD-ESTMD, Fig 8A) or after (ESTMD-EMD, Fig 8B) the matched filter induces strong directionality in the response to a moving target.

Although our EMD stage incorporates a mirror symmetric subtraction unit, which in classical HR-EMDs leads to a full direction opponent response (i.e. an inhibition or opposite sign response to ant-preferred direction motion), neither of the hybrid 2nd order model variants produced negative (opponent) responses. This weak directionality mimics a property observed in biological (small-field) SF-STMD neurons (Barnett et al 2007). In this respect, such neurons contrasted with the strong directional opponency observed in wide-field optic flow neurons that served as the primary inspiration for the HR-EMD model.

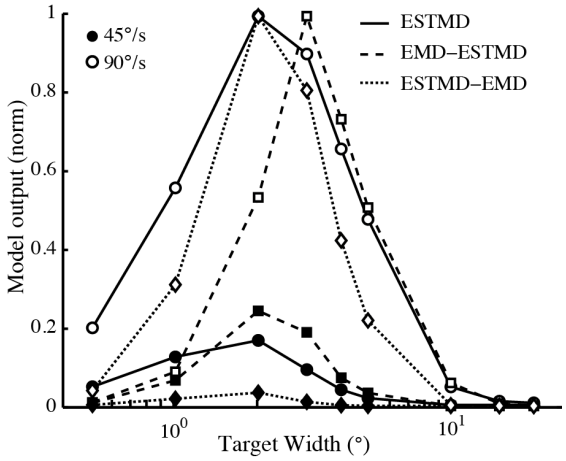

Figure 10. Size tuning of the three model variants at two velocities 45°/s (closed circles) and 90°/s (open circles) shows tuning curves similar to those observed in physiology. The EMD-ESTMD model produces a tuning curve shifted to the right in comparison to the other models. The ESTMD-EMD model has a similar optimum to the ESTMD, however is more sharply tuned.

To examine whether model variants produce similar characteristics to those observed in physiological STMD experiments, we then examined the target size tuning of the model variants by simulating target motion of varying width (i.e. their spatial direction in the direction of travel) and at two different velocities (Figure 10). All 3 model variants produce similar response characteristics, displaying a dependence on both image velocity and target width. The EMD-ESTMD size-tuning curve is sharper and shifted to the right (i.e. less selective for very small targets) than with the other

models. The ESTMD-EMD tuning curve exhibits a similar optimum to the ESTMD model, however is also more sharply tuned. At a lower, less optimal velocity (45°/s), curves are slightly left-shifted compared to a velocity of 90°/s, indicating the confounded relationship between the velocity/width profile of a moving target.

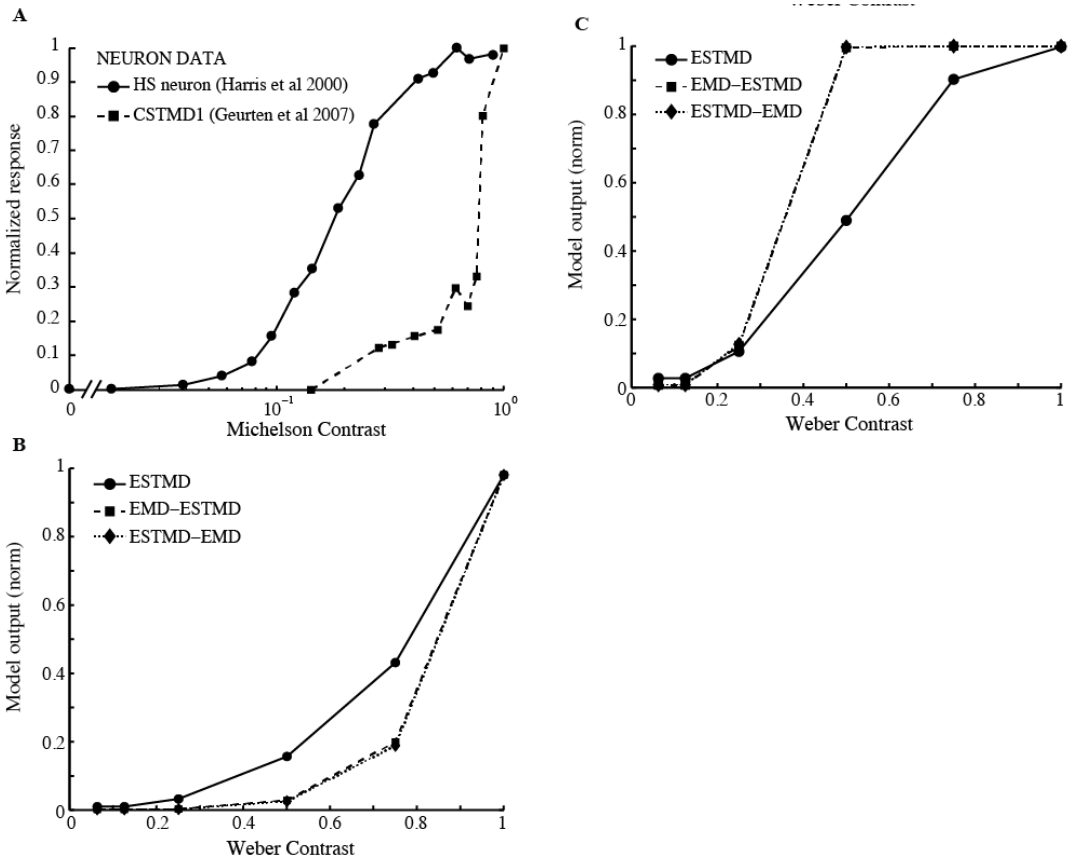

Figure 11: Neuron and Model output in response to moving stimuli of varying contrast. A. Compares the contrast sensitivity function (CSF) for responses to sinusoidal grating patterns of optimum frequency in HS cells, a class of neurons in the fly that are believed to collate the oputput from large arrays of classical HR-EMDs, with those of CSTMD1 (a dragonfly STMD neuron selective for small targets) to optimal target stimuli. Because the wide-field neuron integrates motion from many local EMDs, its sensitivity to low contrast motion is higher than the STMD (hence our selection of a Log axis). However once above threshold, the STMD curve rises more steeply. B. Shows sensitivity of the 3 model variants to Weber contrast $(I_{target}-I_{background})/I_{background}$, a measure appropriate for small targets against a uniform background. Although all 3 variants show an expansive response to contrast, the EMD-ESTMD and ESTMD-EMD models exhibit similar CSFs with a higher-order dependence on contrast (i.e. steeper rise) than the ESTMD, due to the 2nd order (cascaded) multiplicative correlations. C. By applying an arbitrary gain to each of the models (to match the initial expansive 'threshold' for model response) as well as including a saturating non-linearity (a tanh function), we show that the cascaded EMD/ESTMD variants might explain the smaller operating range for STMDs with respect to contrast.

A key characteristic of the HR EMD is that output in response to increased stimulus contrast is expansive, due to the super-linear interaction between the inputs (usually modeled as multiplication). In biological systems, this expansive nonlinearity is inherently bounded by the saturation limits of synaptic signaling and biochemistry within which such super-linear operations must be implemented. Hence typical neurons taking their inputs from HR-type EMDs, such as the HS neurons of flies, show contrast-response functions that are initially super-linear before becoming sub-linear as

saturation begins to dominate the response (Figure 11A). If we model the ESTMD with no such saturation on its outputs (Figure 11B), it displays an identical expansive characteristic, due to the multiplication stage. The EMD-ESTMD and ESTMD-EMD show very similar responses to increasing target contrast. However, as expected from cascading a 2nd order multiplication, the rate of expansion of both is even higher order (i.e. 4thorder) than in the ESTMD.

In this respect, these cascaded EMD/ESTMD models might provide a simple explanation for the pronounced difference in shape of contrast sensitivity functions for insect STMD neurons compared with those of wide-field optic flow neurons which give responses well explained by HR-EMDs (Figure 11A, B). Whereas in Figure 11B we normalize model outputs to their own maximum (at contrast 1.0), in order to compare this expansive nonlinearity across the model variants on a linear contrast scale, we match the initial expansion with arbitrary gains while also including a saturating nonlinearity (hyperbolic tangent), a function that mimics the soft-saturation seen in typical physiological motion detecting neurons (Figure 11C). The resulting curves (Figure 11) suggest that, once we account for response saturation, a 2nd order motion detection operation could explain the hitherto unexplained steeper dependence of contrast sensitivity of STMDs compared with that of wide-field motion detectors (Figure 11A).

4.4 Conclusions

We have shown that several alternative correlation-based models (including the ESTMD) can explain a number of basic response tuning properties of insect STMD neurons, such as their size and velocity tuning. Other characteristics, such as selectivity for contrast polarity (e.g. dark) and their ability to discriminate targets in clutter without relative motion cues, can presently only be explained by the ESTMD model. However, some STMDs also exhibit characteristics that the ESTMD cannot account for, including directionality, facilitation and strongly expansive contrast sensitivity. By elaborating the ESTMD model with a cascaded EMD, we induce directionality (Figure 9) maintain the size and velocity tuning intrinsic to our ESTMD model (Figure 10) and can also explain the highly supra-linear response to target contrast that distinguishes many insect STMD neurons (Figure 11). A 2nd order motion detector network similar to those we implement was previously proposed to explain the 'facilitated' responses observed in some STMDs when targets move along continuous trajectories (Nordström et al 2011, Dunbier et al 2012).

One of our objectives was to determine whether one or other of the cascaded model variants matched observed physiological results and whether in fact one variant could be 'ruled out' due to an inconsistency. As both models match the data we have supported the existence of a 2nd order network, however, more physiological experiments and modeling will be required to elucidate the underlying architecture. In future work it will be interesting to stimulate both the neurons and our model variants with non-Fourier motion and see whether this can be used to determine which architecture is the more likely candidate to underlie STMD processing. In future experiments we will present also moving targets in cluttered environments to our model variants and determine whether this facilitation breaks or enhances target discrimination.

Overall achievements and future work:
In the last decade the Principal Investigators on this project have established the underlying neural machinery of the insect STMD system as an important new model system for computational neuroscience and for bio-inspired models of target tracking. With sponsorship from the US Air Force Office of Scientific Research (Contracts F49620-01-C-0030, FA9550-04-1-0283, and Grants FA9550-09-1-0116 and FA2386-10-1-4114), our research has allowed us to characterize and model key physiological properties that underlie the impressive visual abilities of insects such as predatory dragonflies to discriminate and track small moving targets against cluttered backgrounds, despite poor optical resolution (low pixel count). In the process, we have established a foundational literature on this topic, including a number of high-profile publications in top international journals from this current grant that received substantial media coverage.

As the final project in the series drew to a close, we obtained several significant electrophysiological results that significantly impact our understanding of the processing that underlies small target

detection. These either confirm hypothesized mechanisms or fill in important gaps in our understanding, and the resulting models form an ideal platform for future translational and robotics efforts. They culmination of our modeling effort was a computational model that was highly speculative in the early stages of the project, but which is now on the verge of a mature, explanatory, and physiologically-grounded status.

We remain the world's leading experts on this facet of insect vision, which has heretofore received little attention. Yet feature tracking may be at least as important for visually guided behavior as the better studied and more famous insect wide-field motion analysis (optic flow) system. Furthermore, just as understanding insect optic flow analysis is expected to have a significant impact on visual guidance in autonomous microsystems, so might small target detection for military applications such as seekers and the detection of aircraft for collision avoidance or surveillance purposes.

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4.6 Appendix 1: ESTMD Model description

Model overview

Models were implemented in Matlab (Mathworks, Natick, USA). An overview of early visual processing and the ESTMD model is shown in Figure 12. The EMD model and combination model variants are shown in Figure 1& Figure 8.

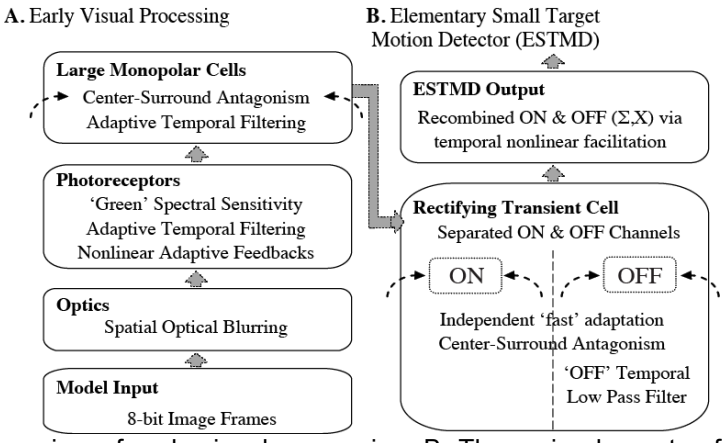

Figure 12: A. Overview of early visual processing. B. The main elements of the elementary small target motion detector (ESTMD). Inputs are spatially blurred to represent fly optics. We retain only the green channel of the RGB image, to represent spectral sensitivity of the motion pathway. A complex photoreceptor model implements dynamic filtering characteristics and adaptive feedbacks which allow for the encoding of vast luminance conditions. LMCs are modeled as dynamic spatiotemporal high-pass filters (relaxed), removing redundant information. The model implements functionality inspired from electrophysiological recordings of RTCs, found in the brain of the fly. This includes ON and OFF channel separation, independent fast temporal adaptation and independent channel surround antagonism. Finally, the delayed OFF channel is recombined with the undelayed ON channel for dark target sensitivity. The final output reveals enhanced small target discrimination as seen in physiological STMDs.

Photoreceptor responses were based on a biomimetic model with parameters and elaborations derived via electrophysiological results from *Eristalis tenax*. The spatiotemporal dynamics of the first order interneurons, the LMCs, have previously been established for blowfly (*Calliphora vicina*) and hoverfly, (*Eristalis tenax*). Model outputs were matched to STMD neurons in *Eristalis tenax*. We then modeled an array of ESTMD (elementary STMD) subunits that could be spatially pooled to form the position invariant receptive field, as seen in the physiological STMD. The model output define values in a three dimensional (2D+t) space.

Early Visual Processing

We used the green channel in our 8-bit input imagery to simulate 'green-blue' spectral sensitivity in the fly visual system. We applied a Gaussian low-pass filter (full width at half maximum 1.4°) to emulate spatial blur of the optics. Input images were spatially sampled at 1° in a hexagonal manner. Photoreceptors incorporated variable gain control, saturating nonlinearities and dynamic low-pass filtering, with cutoff frequencies dependent on adaptation state (ranging from 20 to 100 Hz). This was followed by two divisive, delayed feedbacks (one linear, one exponential) representing short and longer term adaptations (τ = 23 ms, τ = 12.4 s). Finally, a compressive, saturating nonlinearity is implemented by a Naka-Rushton transform. The LMC implements spatiotemporal high-pass filtering, altering its filtering characteristics dependent on visual conditions. In the dark adaptation state, the LMC is more integrative with longer sustaining temporal components. As overall luminance conditions increase, the LMC becomes more transient and high-pass in nature, both in space and time. This spatial interaction (center-surround antagonism) was modeled in a feed forward manner with surround (nearest neighbor) photoreceptor signals summed, and temporally delayed (τ=16 ms), before subtractively inhibiting the central LMC (strength ranging from 0-30%, dependent on adaptation state). The LMC temporal dynamics were modeled with relaxed, variable high-pass filtering (lower corner frequency ranging from 0 to 8 Hz) which incorporated a small DC component (0-10%). Following, a saturating nonlinearity with a hyperbolic tangent function, ensured the LMC response was limited to a predictable output range.

Elementary Small Target Motion Detector (ESTMD)

The main processing of the ESTMD is based on the Rectifying Transient Cell (RTC). Briefly, the RTC creates transient 'on' and 'off' phases (from the LMC high-pass filtering), separated via a further temporal high pass filter (τ = 40ms) and then half-wave rectification into independent ON and OFF channels. Each of the channels is temporally processed through a fast adaptive mechanism. An adaptation state is determined by a nonlinear filter, which approximates cellular 'fast depolarization and slow repolarization' responses. This low-pass filter switches its time constant dependent on whether the input is increasing or decreasing (time constants are 'fast' (τ = 3 ms) when channel input is increasing and 'slow' (τ = 70 ms) when decreasing). This adaptation state subtractively inhibits the unaltered 'pass-through' signal. The result of this complex, nonlinear filtering is the signaling of 'novel' transient contrast changes (of the particular channel phase, 'on' or 'off') with the suppression of fluctuating textural variations. As well as this temporal antagonism, the channels also exhibit spatial antagonism with ON surround channels subtractively inhibiting the ON centre channel, and similarly with the OFF channels. The resultant signal was then half-wave rectified, so that the surround does not inhibit the centre below a zero value (a nonlinearity seen in some spiking neurons). ON and OFF channels are recombined via multiplication [6]. Both dark and light target sensitivity is possible by delaying and recombining the relevant contrast polarity. For these experiments we delayed the OFF channel using a 1^{st}-order low-pass filter (τ= 25 ms) and multiplying this by the undelayed ON channel. This processing provides a template for the characteristic temporal 'signature' of a small moving target.

Elementary Motion Detector (EMD)

The 2-Detector Elementary Motion Detector (EMD) as described by Eichner et al.(2011) and Joesch et al. (2013) was implemented as described above (Figure 1). Channels were separated into ON and OFF channels via half-wave rectification following high pass filtering (τ=100 ms). The delay arm was modeled with a low-pass filter (τ= 25 ms).

5. List of Publications arising from this grant:

Papers listed are only those supported either in full or in part by the present grants FA2386-10-1-4114 (University of Adelaide, PI O'Carroll) & FA9550-09-1-0116 (Tanner Research Inc. PI Shoemaker). All papers acknowledge the AFOSR support for this project. 3 early papers in this list (indicated with a *) arose from this project but cite the support of the preceding contract within the 3-year project, i.e. the base period (FA 2386-09-1-4058).

5.1 Refereed papers by the principals with full support from this grant

1. Wiederman, S.D., Shoemaker, P.A., & O'Carroll, D.C. (2013) Correlation between OFF and ON channels underlies dark target selectivity in an insect visual system. In 2nd revision, Journal of Neuroscience, ms# JN-RM-1277-13R1 (as this was a 2nd resubmission addressing only minor comments, we expect that this paper will be formally accepted shortly)
2. Wiederman, SD and O'Carroll DC (2013) Biomimetic Target Detection: modeling 2nd order correlation of OFF and ON channels. Proc. of the IEEE, Symposium Series on Computational Intelligence for Multimedia, Signal and Vision Processing, Singapore (in press).
3. Wiederman, S.D. & O'Carroll, D.C. (2013) Selective attention in an insect neuron. Current Biology. 23: 156-161 DOI: 10.1016/j.cub.2012.11.048
4. Dunbier, James R.; Wiederman, Steven D.; Shoemaker, P.A. & O'Carroll, D.C. (2012) Facilitation of dragonfly target-detecting neurons by slow moving features on continuous paths. Frontiers in Neural Circuits 6: DOI: 10.3389/fncir.2012.00079
5. Halupka, K.J., Wiederman, S.D., Cazzolato, B.S. & O'Carroll DC (2011) Discrete Implementation of Biologically Inspired Image Processing for Target Detection. ISSNIP 2011. Proceedings of IEEE 2011 7th International conference on Intelligent Sensors, Sensor Networks and Information Processing, pp. 143-149 doi: 10.1109/ISSNIP.2011.6146617
6. Wiederman, S.D., & O'Carroll DC (2011) Modeling Inhibitory Interactions Shaping Neural Responses of Target Neurons to Multiple Features. ISSNIP 2011. Proceedings of IEEE 2011 7th International conference on Intelligent Sensors, Sensor Networks and Information Processing, pp. 73-79 doi: 10.1109/ISSNIP.2011.6146547
7. Dunbier, J.R., Wiederman, S.D., Shoemaker, P.A. & O'Carroll DC (2011) Modelling the Temporal Response Properties of an Insect Small Target Motion Detector. ISSNIP 2011. Proceedings of IEEE 2011 7th International conference on Intelligent Sensors, Sensor Networks and Information Processing, pp. 125-130 doi 10.1109/ISSNIP.2011.6146600
8. Shoemaker, P. A. (2011) "Multicompartment Simulations of NMDA Receptor-Based Facilitation in Insect Visual Neurons", Proceedings of IEEE 2011 7th International conference on Intelligent Sensors, Sensor Networks and Information Processing, pp. 125-130 doi 10.1109/ISSNIP.2011.6146600
9. Wiederman, S.D. & O'Carroll, D.C. (2011) Discrimination of features in natural scenes by a dragonfly neuron. J. Neurosci. 31: 7141-7144
10. Nordström, K, Bolzon, D.M. & O'Carroll, D.C. (2011) Spatial facilitation by a high-performance dragonfly target-detecting neuron. Biology Letters. published online ahead of print 26 January 2011 doi: 10.1098/rsbl.2010.1152
11. Wiederman, S.D., Brinkworth, R.S.A & O'Carroll, D.C. (2010) Performance of a bio-inspired model for the robust detection of moving targets in high dynamic range natural scenes. Journal of Computational and Theoretical Nanoscience 7: 1-10 doi:10.1166/jctn.2010.1438

12. *Bolzon, DM, Nordström, K & O'Carroll, DC (2009) Local and Large-Range Inhibition in Feature Detection. Journal of Neuroscience 9(45): 14143-14150; doi:10.1523/JNEUROSCI.2857-09.2009

13. *Nordström, K & O'Carroll, DC (2009) Feature Detection and the Hypercomplex Property in Insects. Trends in Neurosciences 32:383–391 doi:10.1016/j.tins.2009.03.004

* n.b. these 2 earliest papers from this project formally acknowledge the partial support of the base period project (FA 2386-09-1-4058).

5.2 Papers by the Principals in Related Areas (all with partial support from this grant)

14. O'Carroll, DC, Barnett, PD & Nordström, K (2012) Temporal and spatial adaptation of transient responses to local features. Frontiers in Neural Circuits 6: 74 DOI: 10.3389/fncir.2012.00074 (ISI IF=5.35, Percentile rank: 98%)

15. O'Carroll, DC, Barnett, PD & Nordström, K (2011) Local and global responses of insect motion detectors to the spatial structure of natural scenes. Journal of Vision 11 (14) art # 20, doi: 10.1167/11.14.20

16. Nordström, K, Moyer de Miguel, IM, & O'Carroll, DC (2011) Rapid contrast gain reduction following motion adaptation. J. Exp. Biol. 214 (23), pp 4000-4009 doi: 10.1242/jeb.057539

17. O'Carroll, D.C., Barnett, P.D., & Nordström, K (2011) Computational models reveal non-linearity in integration of local motion signals by insect motion detectors viewing natural scenes. ISSNIP 2011. Proceedings of IEEE 2011 7th International conference on Intelligent Sensors, Sensor Networks and Information Processing, pp. 131-136 doi: 10.1109/ISSNIP.2011.6146601

18. O'Carroll, D.C., & Warrant, E.J. (2011) Computational models for spatiotemporal filtering strategies in insect motion vision at low light levels. ISSNIP 2011. Proceedings of IEEE 2011 7th International conference on Intelligent Sensors, Sensor Networks and Information Processing, pp. 119-124 doi: 10.1109/ISSNIP.2011.6146593

19. Shoemaker, P. A., Hyslop, A. M., & Humbert, J. S (2011). "Optic Flow Estimation on Trajectories Generated by Bio-Inspired Closed-Loop Flight." Biological Cybernetics, Vol. 104, No. 4, pp. 339-350; doi: 10.1007/s00422-011-0436-8, 2011

20. Shoemaker, P. A. (2011) *"Neural Bistability and Amplification Mediated by NMDA Receptors: Analysis of Stationary Equations".* Neurocomputing, doi: 10.1016/j.neucom.2011.04.01.

21. **Barnett, P.D., Nordström, K*, & O'Carroll, D.C. (2010) Motion adaptation and the velocity coding of natural scenes. Current Biology. 20: 994-999 doi:10.1016/j.cub.2010.03.072

* n.b. this earliest paper from this project formally acknowledge the partial support of the base period project (FA 2386-09-1-4058).

5.3 Other Conference presentations (some including published abstracts)

22. Wiederman SD, Dunbier JR & O'Carroll DC (2013) Modulating selective attention in an insect neuron, 30th Annual Meeting of the Australiasian Neuroscience Society, Melbourne, February. 3-6

23. Wiederman, S.D., Shoemaker, P.A., & O'Carroll, D.C. (2013) Modeling selective attention in an insect visual neuron. 6th Australian Workshop on Computational Neuroscience (NeuroEng 2013), The University of Melbourne, 30-31st January, 2013

24. Wiederman SD and O'Carroll DC (2012). Feature saliency in a dragonfly neuron. Front. Behav. Neurosci. Conference Abstract: 10th International Congress of Neuroethology. doi: 10.3389/conf.fnbeh.2012.27.00223 Received: 30 Apr 2012; Published Online: 07 Jul 2012

25. O'Carroll D, Bolzon D and Nordström K (2012). Bar cells: a novel class of insect feature detector. Front. Behav. Neurosci. Conference Abstract: Tenth International Congress of Neuroethology. doi: 10.3389/conf.fnbeh.2012.27.00236 received: 30 Apr 2012; Published Online: 07 Jul 2012

26. Nordstrom K, Bolzon D and O'Carroll D (2012). Bar cells: Underlying neuro-physiological mechanisms. Front. Behav. Neurosci. Conference Abstract: Tenth International Congress of Neuroethology. doi: 10.3389/conf.fnbeh.2012.27.00279 Received: 30 Apr 2012; Published Online: 07 Jul 2012

27. Dunbier JR, Wiederman SD and O'Carroll DC (2012). Predictive response facilitation to moving targets in an insect neuron. Front. Behav. Neurosci. Conference Abstract: Tenth International Congress of Neuroethology. doi: 10.3389/conf.fnbeh.2012.27.00234 Received: 30 Apr 2012; Published Online: 07 Jul 2012

28. O'Carroll D.C. (2011) "*Neural mechanisms underlying small target discrimination by insects"*, 3nd International Conference on Fly Vision, Howard Hughes Medical Institute, Janelia Farm, Virginia, USA

29. Wiederman S.D., Dunbier J.R., & O'Carroll D.C. (2011) *"Inter-hemispheric inhibitory connections of a feature-discriminating neuron in the dragonfly (Hemicordulia tau),* 31st Annual Meeting of the Australian Neuroscience Society, Auckland, New Zealand, Jan. 2011

30. Dunbier J.R., Wiederman S.D. and O'Carroll D.C. (2011) *"Local facilitation of dragonfly hypercomplex neurons"* 31st Annual Meeting of the Australian Neuroscience Society, Auckland, New Zealand, Jan. 2011

31. Wiederman S.D., Dunbier J.R., & O'Carroll D.C. (2011*) "Size tuning of intra and inter-hemispheric inhibitory connections of a feature discriminating neuron in the dragonfly".* 8th IBRO World congress of neuroscience. International Brain Research Organization. Florence, Italy, July 14 2011.

32. O'Carroll D.C. "*Neural processing of form and motion by the insect visual system*". Australia. Invited presentation, Vision 2010: From Photoreceptors to Behaviour, Friday, 29 January & Saturday, 30 January 2010, A satellite meeting to the 2010 joint meeting of the Australian Neuroscience Society and the Australian Physiological Society

33. Dunbier J.R., Bolzon D.M., Wiederman S.D., Shoemaker, P.A., Nordström K. & O'Carroll D.C. (2010) "Facilitation in hyperacuity of dragonfly hypercomplex neurons." Poster # POS-TUE-156, 30th Annual Meeting of the Australian Neuroscience Society, Sydney, January 2010

34. Barnett P.D., Nordström K. & O'Carroll D.C. (2010) Local motion detection: temporal and spatial modulation of gain and transient responses to features in natural images. Poster # POS-MON-195, 30th Annual Meeting of the Australian Neuroscience Society, Sydney, January 2010

6. New Discoveries, Inventions, or Patent Disclosures

None this period, beyond the findings reported above, or documented in the previous reports and the above publications. A separate DD882 report is attached.