Biomimetic Visual Detection Based on Insect Neurobiology

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ABSTRACT

With a visual system that accounts for as much as 30% of the lifted mass, flying insects such as dragonflies and hoverflies invest more in vision than any other animal. Impressive visual performance is subserved by a surprisingly simple visual system. In a typical insect eye, between 2,000 and 30,000 pixels in the image are analyzed by fewer than 200,000 neurons in underlying neural circuits. The combination of sophisticated visual processing with an approachable level of complexity has made the insect visual system a leading model for biomimetic approaches to computer vision. Much neurobiological research has focused on neural circuits used for detection of moving patterns (e.g. optical flow during flight) and moving targets (e.g. prey). Research from several labs has led to great advances in our understanding of the neural mechanisms involved, and has spawned neuromorphic hardware based on key processes identified in neurobiological experiments. Despite its attractions, the highly non-linear nature of several key stages in insect visual processing presents a challenge to understanding. I will describe examples of adaptive elements of neural circuits in the fly visual system which analyze the direction and velocity of wide-field optical flow patterns and the result of experiments that suggest that these non-linearities may contribute to robust responses to 'natural' image motion.

Keywords: Biomimetic Vision, Visual Processing, Motion Detection, Target Detection, Insect Vision

1. INTRODUCTION

The control and guidance of movement of an animal or robot through a structurally complex world is a task that presents enormous computational challenges and yet requires real-time solutions. One need only to observe a hoverfly make a perfectly controlled landing upon a flower moving in the breeze, to realize that these problems are solved by even simple biological systems. Many insects engage in elaborate visually guided behavior, ranging from precise hovering flight, to spectacular aerial pursuit of other insects. With sophisticated visual behavior and yet a brain with (typically) fewer than 200,000 neurons, the insect visual system provides an attractive model system for investigating a variety of basic questions about visual processing of great interest to engineers. The relatively small scale (between 2,000 and 30,000 pixels in a typical insect eye) and comparative simplicity of the insect visual system suggest that it may be possible to implement similar visual processing with analog circuits using contemporary microelectronic technology. Biomimetic approaches to development of electronic guidance components, based on models of insect visual processing, are now increasingly practical not just because of advances in silicon based engineering, but because of knowledge gained through extensive basic research on the biological system in recent years. Much of this neurobiological research has focused on neural circuits used for detection of moving patterns (e.g. optical flow during flight) and moving targets (e.g. prey). Research from several labs has led to great advances in our understanding of the neural mechanisms involved, and has spawned 'neuromorphic' hardware based on key processes identified in neurobiological experiments.

I review here the key stages of visual processing in insect neural pathways devoted to processing optic flow information and motion of moving targets. Despite its attractions, the highly non-linear nature of several key stages in these pathways presents a challenge to understanding, modeling and development of neuromorphic hardware. I will describe examples of

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adaptive elements in neural circuits of the insect visual system and our progress towards biomimetic models for these neural pathways.

2. OPTICS AND EARLY VISUAL PROCESSING

2.1 Ommatidial Organization and Spatial Filtering

Although several different types of imaging principles are common amongst insect compound eyes, the most familiar and common type, found in many day active insects (including flies and dragonflies) is the apposition eye, illustrated schematically in figure 1. In this type of eye, each 'pixel' at the focal plane exists as a small group of (typically 8) photoreceptor neurons (illustrated here by a single neuron for each lens) often fused into a single light guide (the *rhabdom*) in the retina. In typical eyes of day-active insects, each rhabdom is 1-2 micrometers in diameter. An image is formed at the tip of the rhabdom by refraction occurring primarily at a miniature corneal facet lens, unique to each rhabdom. Such a lens/receptor group is called an *ommatidium*, each of which is directed at a unique axis in space. Because the optical axis of each ommatidium is independent of its neighbors, the fields of view of adjacent ommatidia can overlap. Combined with optical diffraction at the small diameter (typically 30 micrometers) lens in each ommatiium, this introduces significant spatial low-pass filtering into this first stage of processing.

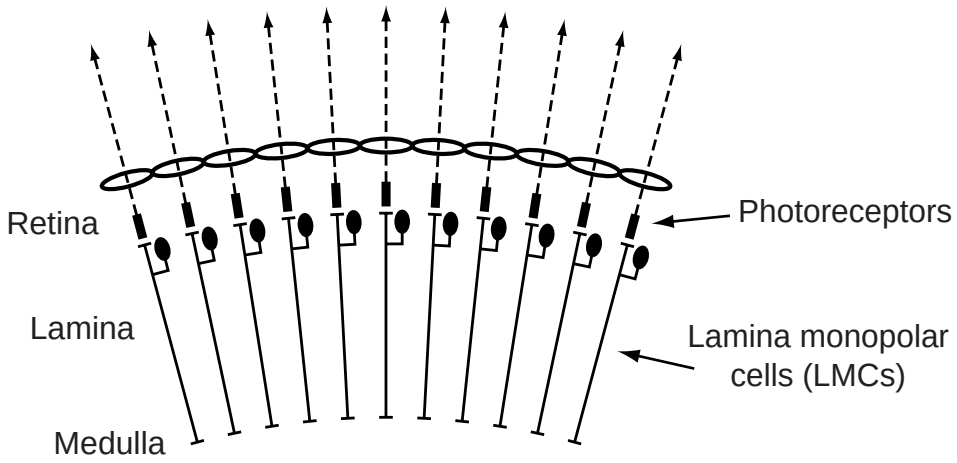

Figure 1. Schematic view of the basic optical mechanism and first levels of connectivity in a typical insect visual compound eye of the apposition type.

Phototransduction in each neuron is mediated by a light-sensitive pigment, *rhodopsin*, that triggers a flux of ions and a graded (analog) voltage change across the membrane with a magnitude that depends on the amount of light absorbed. Photoreceptors then make an electrochemical synapse with several different second-order neurons, the best known of which are the *Lamina monopolar cells* (LMCs) in the first optic ganglion, usually termed the *Lamina*. These neurons preserve the retinotopic map of space at the level of ommatidia, as do higher order neurons to which they connect in the second optic ganglion, the *Medulla*.

2.2 Temporal Filtering in Early Vision

The vast majority of our knowledge of the functional properties of these 'early' visual neurons comes from the technique of single-neuron intracellular recording, using 'sharp' recording electrodes. The recording electrode is a hollow glass micropipette with a fine tip (ca. 100 nm tip diameter), filled with high concentration salt solution. By inserting the electrode

into the cytoplasm of single neurons, it is possible to correlate voltage changes across the cell membrane with visual stimuli presented within the receptive field of the neuron. Figure 2 illustrates such recordings from photoreceptors and LMCs in neurons of a hawkmoth (Sphingidae) in response to a transient (impulsive) flash of light from an LED. At very low contrasts, such impulse responses increase in magnitude linearly with intensity, and can thus be regarded as linear filter kernels for the temporal filtering induced by phototransduction and the passive resistive and capacitive properties of the neuronal membrane. The monophasic impulse response and Bode plots (fig. 2b) show that, under these conditions, photoreceptors are temporal low-pass filters. The synapse between photoreceptors and the LMCs has high-pass properties, so that LMCs have an approximately zero-mean biphasic impulse response and yield band-pass Bode plots (figure 2 lower).

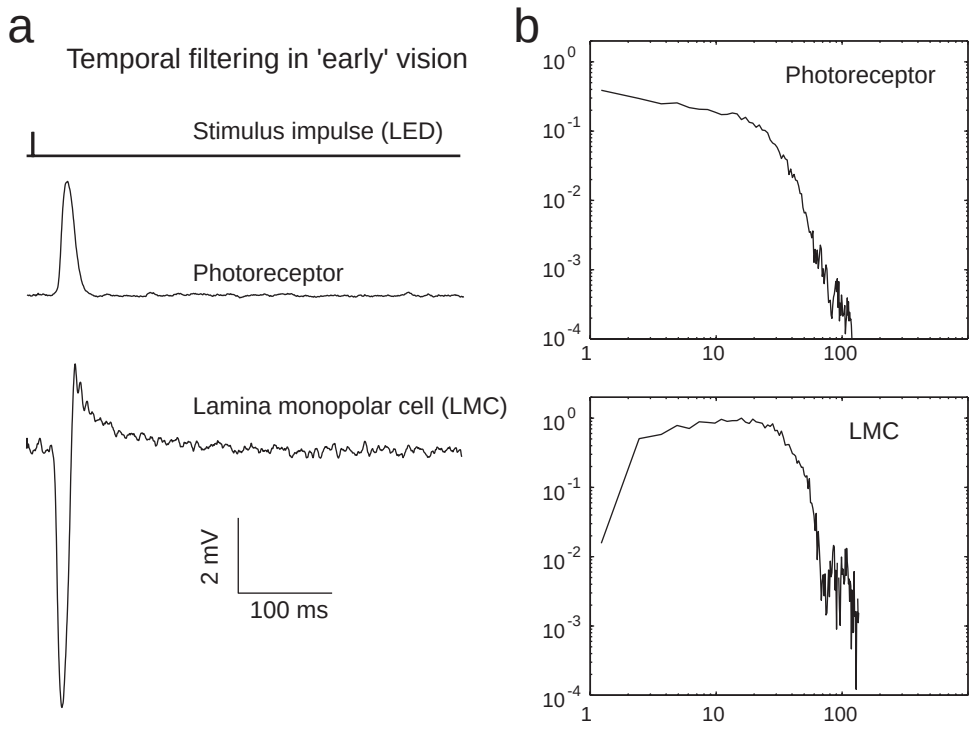

Figure 2. Temporal filtering properties of neurons in early vision. A shows the impulse responses of 1st order (photorectpors) and 2nd order (Lamina monopolar cells) recorded intracellularly from the eye of a hawkmoth (*Manduca sexta*). B shows Bode plots obtained by Fourier transforming the impulse responses. The slow kinetics of phototransduction and membrane properties in the photoreceptors provides significant low-pass temporal filtering.

Recent work[1] has investigated responses of these neurons in flies to higher contrast stimuli derived from natural scenes[2], and underscores the importance of additional, non-linear processing even at the earliest stages of vision. A number of underlying biochemical and biophysical properties of photoreceptors, including 'self-shunting' and saturation of the phototransduction mechanism lead to an overall logarithmic compression in the coding of intensity. In addition, adaptive properties operating at a variety of time-scales greatly extend the range of luminances encoded by both photoreceptors and LMCs. Some of these act rapidly enough that 'internal' contrast within local patches of natural scenes are either enhanced or compressed as appropriate during natural, rapid flight within a complex scene[1]. This adaptive behavior at high contrasts is not captured by the impulse responses illustrated in figure 2.

3. HIGHER ORDER VISUAL PROCESSING

Beyond the Lamina, neural processing diversifies into a number of 'vertical' pathways within the 2rd optic ganglion, the *Medulla*. Neurons at this level are less well studied than those of the lamina, due mainly to their very small size, which prohibits reliable sharp electrode recording. The retinotopic projection from rhabdom to lamina 'cartridge' is preserved in the medulla, with a large number (possibly in excess of 50 in some species) of local neurons receiving synaptic input from lamina neurons, suggesting a diversification of information into parallel pathways, most of which remain completely unstudied. In addition to tiny 'local' neurons, the medulla contains a diverse range of 'horizontal' neurons with dendrites that spread across the cartridge-like organization of the medulla and which probably mediate interactions between local points in the neural 'image'. Because of the paucity of data from direct recordings, most of what we understand about specific neural pathways at this level is inferred from recordings at their outputs to larger neurons in the 3rd optic ganglion, the *lobula* complex. In the lobula, the outputs of small, 'local' medulla neurons are integrated by 'collator' neurons, which make synaptic contacts with a large number of medulla cells, many of which send outputs into the lobula. These cells are often called 'tangential neurons' because the synaptic contacts are made within large tree like 'arborizations' that are tangential to the 'vertical' information flow within columnar (serial) pathways. Many tangential neurons have large axons and are amenable to sharp electrode intracellular recording. Individual tangential neurons have been recorded from repeatedly in different individuals of one species and identified anatomically by dye injection through the recording electrode, and have subsequently been 'named' in a manner which usually reflects their physiology (e.g. VS1=vertical System motion sensitive cell 1). In addition to tangential neurons, the lobula complex also contains many local 'columnar' neurons, the vast majority of which have never been studied physiologically.

I will concentrate here on the properties of two classes of tangential neurons at this level. One class are typified by the so-called Horizontal System (HS) neurons of the *lobula plate*, a specialized sub-region of the lobula complex present in some insect groups, notably in two-winged (dipteran) flies. These neurons (among the best studied neurons of any animal) mediate compensatory responses of the insect to horizontal, rotational image motion (yaw) across a wide receptive field and are part of a system of related neurons believed to be critical for flight control and stabilization[3,4]. The second class of neurons form part of an (as yet) poorly understood pathway involved in analysis of the motion of small targets, in the remaining part of the the lobula complex, simply termed *lobula* in most insects. I use the generic term 'small target movement detector' (STMD) to classify these neurons, since they can be distinguished from other tangential neurons on the basis of a remarkable selectivity in response for very small, moving targets. Despite the use of this term to categorize these neurons, it is by no means clear at this stage whether they represent a single class of 'target detector' at all, or even whether they serve a functional role for target detection. Nevertheless, many of the insects in which such neurons have been found so far (dragonflies and dipteran flies, including hoverflies) display specialized behavior that involves tracking of small moving targets, either conspecifics (mates or potential mates) or prey. It seems very likely that these STMD neurons are a key element of this behavior. Of particular interest from the point of view of biomimetic modeling of insect visual processing, is the fact that some insects (dragonflies in particular) have been shown to execute sufficiently sophisticated analysis of moving targets to permit calculation of an intercept course[5,6].

3.1 Motion Analysis by HS Neurons

The neural pathway involved in wide-field motion analysis in insects has attracted intense interest over the last 40 years. Indeed, one of the first, and undoubtedly among the most enduring biomimetic models for motion detection, the Hassenstein-Reichardt correlation scheme, was first described over 40 years ago after study of the turning responses of a weevil tethered in a visual stimulus arena[7,8]. This study exploited the *optomotor* response – the tendency of most insects to turn in response to wide-field motion, in the same direction as the motion (syn-directional torque response), presumably on the assumption that rotation of the surrounding world must result from deviation in the insects own desired path (self motion). The model is based on a non-linear *correlation* of the 'response' of one pixel with the delayed response of a neighboring pixel[7,8]. Such local correlation between the same two pixels is also carried out in reverse (mirror sub-unit), and the two outputs are then subtracted to form a local 'elementary motion detector' (EMD) that is selective for a unique direction of local motion. Hassenstein and Reichardt[7] proposed that the outputs of a large array of such correlation type EMDs are then summed across a large array to produce the observed turning responses of the insect (figure 3).

Subsequent physiological analysis of neurons involved at various levels of the insect visual system has provided convincing evidence for a mechanism similar to that proposed on the basis of this early behavioral work. Bandpass filtering by the photoreceptors and LMCs in early vision approximate the linear spatiotemporal filters that Hassenstein & Reichardt proposed as inputs to the EMD[7,8]. It is now generally accepted that the EMDs themselves likely exist at the level of the medulla or distal lobula (figure 3). While some likely candidates for weakly direction-selective local motion detector have been identified[9], the evidence for identity of fully opponent local EMDs remains controversial. Nevertheless, many predictions of the model are supported by recordings from HS neurons and other tangential neurons of the insect lobula plate using both local and global motion stimuli. Recent data suggests that individual HS neurons and other classes of tangential neurons sum local EMDs with local preferred directions for motion in such a way that they are matched filters for specific classes of complex optic flow such as rotation or expansion[10,11].

3.1.1. Neuromorphic models for wide-field motion detection

With recent interest in 'neuromorphic' modeling of biological functions in analog VLSI technology, there have been a number of efforts to emulate visual motion detection. Among these have been experimental implementations of insect-inspired elementary motion detection models in analog integrated circuits[12,13,14,15].

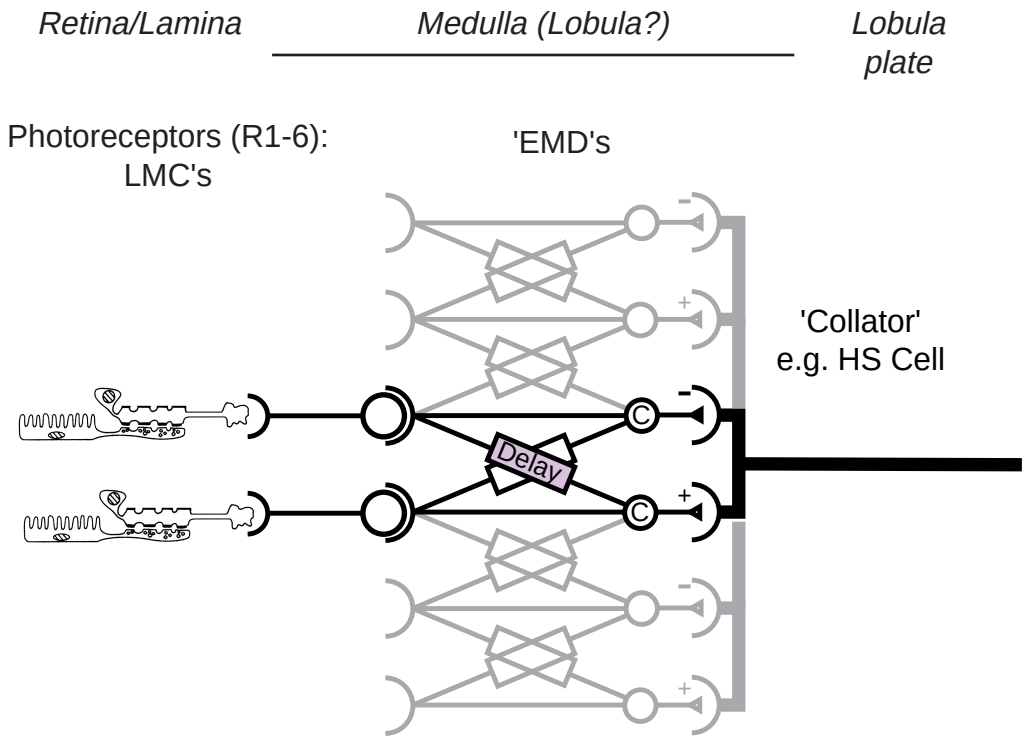

Figure 3. A schematic representation of the pathway believed to be involved in motion analysis by collator neurons in the lobula plate of dipteran flies, such as HS neurons.

Despite the wealth of data supporting the model proposed by Hassenstein & Reichardt, and its attractiveness for silicon modeling, the original model is, with the exception of the essential non-linearity of the correlation operation (C in figure 3) composed entirely of cascaded linear filtering operations. In this respect, it is a great oversimplification of the biological system, which, as already noted in section 2.2., is significantly non-linear at even the earliest levels.

3.1.2. Motion adaptation in HS Neurons

A major non-linearity, inconsistent with existing models for motion detection, is the phenomenon of motion adaptation, first described from the H1 tangential neuron of the fly lobula plate[16]. Motion adaptation is characterized by a decrease in the response of the neuron to sustained presentation of the same moving pattern, and an increase in response modulations by changes in the velocity of the moving pattern, neither of which are predictions of the basic EMD model. Maddess[16] showed that this adaptive phenomenon is a local property of the motion detectors and thus likely to occur prior to 'collation' of EMD outputs by tangential neurons. Subsequent work[17,18] suggested that the site of adaptation was the time constant of the delay filter within the EMDs, a model which was subsequently formalized as the 'adaptive Reichardt model'[19] in which the EMD outputs are fed back to reduce the delay filter time constant. This model has already been incorporated into experimental approaches to analog VLSI[13]. A non-adaptive EMD can be regarded as a complex spatiotemporal filter that responds best over a limited range of velocities. The adaptive model is attractive from a biomimetic perspective because it has an extended dynamic range in the velocity domain compared with a non-adapting EMD model, without the complexity that would be required were two or more EMDs with different spatiotemporal optima to be summed. Adaptation of this kind serves to maintain large response modulation by transient velocity changes even when the velocity of ambient image motion exceeds the inherent 'optimum', as the shorter time constant 'retunes' the EMD to higher image speeds.

We have recently subjected key predictions of this adaptive model to rigorous testing using physiological recordings from HS neurons. Interestingly, we find no evidence for any adaptation of the delay filter time constant consistent with this model[20,21,22]. Instead, our data suggest that the time constant of the delay filter is inherently short, providing maximal sensitivity to high velocities in an unadapted state. Detection of non-optimal low velocities required for behaviors such as stabilization during hovering flight seems to be served primarily by inherently high gain in the unadapted state[21,22], combined with relatively good optics in species which hover well, which permits detection of relatively high spatial frequencies[23,24]. Motion adaptation instead seems to operate as a gain control, reducing the effects of saturation that would otherwise result from this configuration at 'optimal' intermediate and high velocities[22].

We have now suggested[25] tentative new models for motion adaptation, based on these recent findings, in which the EMD output is fed back as in the earlier adaptive EMD model, but instead of altering the delay time constant, the feedback operates to reduce the feed-forward gain of the EMD. We propose that a possible additional advantage of this configuration is a reduced sensitivity of the EMD to the local contrast of an image, in addition to the extended dynamic range captured by the earlier adaptive models. This 'higher order' adaptive feedback, combined with additional non-linear adaptive properties of early vision (as modeled by van Hateren and Snippe[1]), may provide more robust responses to different patterns (or patches within a pattern) moving at the same velocity, and thus improve the encoding of optic flow. Our new model is amenable to implementation in analog VLSI and our ongoing efforts aim to develop this to a practical implementation of a robust adaptive EMD based on this principle.

3.2 Responses to Moving Targets by STMD Neurons

As mentioned earlier, a major class of neurons in the insect lobula displays sensitivity to very small moving targets, subtending just one or two facets of the compound eye, and moving with respect to background within their receptive fields. These were first described in dragonflies[26], an group of insects that chase prey on the wing[5] and use visual cues to estimate its course and intercept its flight path[6] . Similar cells have now also been described from hoverflies[27,28,29], another highly visual and aerobatic insect that engages in high speed pursuit behavior. STMDs of both insect groups typically have frontal or dorsal receptive fields that correspond to the zone of highest acuity in the eye, where inter-ommatidial angles may be as small as 0.5 degrees.

Cells classifiable as STMDs appear to be organized hierarchically in terms of receptive field size. They include neurons with relatively small receptive fields, corresponding to 50-100 overlying facets and a few degrees of visual angle[27,28,29,30]. These 'small-field' cells seem to be retinotopically organized, so that they may be used to signal the position of targets[27]. Others have receptive fields that may span the entire visual hemisphere[30]. The cells with largest receptive fields tend to have the most 'highly tuned' response properties, characterized by no spontaneous firing activity, and no response to 'non-preferred' targets such as bars, edges or grating patterns (Figure 4). These cells do, however, respond very strongly to small targets (down to 0.5 x 0.5 degrees) that move at any location within their receptive field.

Cells with smaller receptive fields also tend to display distinct response maxima at the center of those fields, and show evidence of spatially distinct (often asymmetrically offset) inhibitory 'surround' regions. Individual neurons of both groups may be insensitive to the direction of target motion, but are more typically direction sensitive, and display a distinct velocity optimum, suggesting that they may receive input from correlation-type EMDs.

Further work is required to establish whether the larger and smaller field classes of STMD are serially hierarchical, with the small receptive field units representing 'elementary small target motion detector' (ESTMDs) pre-synaptic to large field 'collator' cells, by analogy to the HS neurons of the lobula plate. The data obtained so far are, nevertheless, consistent with this hypothesis. In particular, most large field STMDs studied so far exhibit profound non-linear adaptation to local target motion. This adaptation is long lasting, and limited only to those parts of the receptive field that are repeatedly stimulated by target motion, suggesting adaptation of local neurons on the input pathway. Furthermore, such adaptation is not induced by stimuli that the STMD does not respond directly to, such as wide-field motion or high-contrast flicker. Indeed, such stimuli may serve to 'refresh' local sensitivity to target motion in parts of the receptive field that had previously been adapted (dishabituation). Since such stimuli are likely to recruit adaptive mechanisms in early visual neurons or EMDs that feed wide-field motion detectors (see section 3.1.2), this finding suggests that the local, adapting neurons are already 'tuned' to target motion.

Many of these STMDs have inputs in the lobula complex but send outputs to the lateral mid-brain and the suboesophageal ganglion. As such, it is possible that some of them may synapse with a small group of well described target sensitive descending neurons (TSDNs) that connect to steering muscles in the insect's thorax[5,6,31]. Electrical stimulation of these TSDNs produces steering movements of the wings, suggesting that they are involved in steering flight towards moving targets[5,6].

3.2.1 Biomimetic models for moving target detection

Models for the processing of STMDs are emerging from the mass of new data that we are obtaining for these neurons, but remain tentative. In the blowfly lobula plate, a model has been proposed to explain the size selectivity for a class of tangential neurons, the so called 'figure discrimination' or FD cells[32,33]. These neurons, like the STMDs of the lobula, respond best to relatively local motion stimuli, although they are far less selective for very small target motion. Selective ablation studies (using a laser to destroy key neurons suspected of a role in mediating size tuning of these cells)[33] suggests a relatively simple mechanism in which a feedforward 'collator' (similar to an HS cell) sums local EMD outputs, while a similar neuron, sharing an identical receptive field feed, provides inhibitory feedback. As the size of the moving stimulus increases, so does the strength of inhibition, thus suppressing the response.

Our most recent data for STMDs[30], however, suggests that their extreme selectivity for very small targets derives from more complex feedforward and feedback inhibitory mechanisms than those that seem to explain size preference in the FD cells. Important evidence for this comes from 'raw' responses recorded intracellularly to motion of dark bars of different length (figure 4), moved against a blank background. In many recordings, the tip of the electrode lies in the main axon of the neuron, and we see only the bi-phasic action potentials that propagate actively along the axon to the output synapses made onto the next neuron in the pathway. We can think of these action potentials as encoding the output of the neuron. In some recordings, however, the recording electrode is close enough to the synaptic inputs that we are able to observe action potentials 'riding' on the underlying post-synaptic noise of the neuron (excitatory post-synaptic potentials or EPSPs and their inhibitory counterparts, IPSPs). Individual EPSPs and IPSPs are visible as discrete 'bumps' in membrane potential casused by quantal release of neurotransmitter onto the STMD if the stimuli are sufficiently subtle. Since action potentials are only elicited by post-synaptic events which depolarize the membrane above threshold (excitatory post-synaptic potentials or EPSPs) such recordings provide a unique opportunity to see the relationship between post-synaptic potentials (inputs) and spike generation (outputs).

When the stimulus is a very small target, we see a barrage of EPSPs that sum to a sustained depolarizing (DC) stimulus (figure 4 upper traces). This excites a vigorous train of action potentials from the STMD, which 'ride' on the EPSPs. As the target size increases, we see individual EPSPs competing with hyperpolarizing inhibitory post-synaptic potentials (IPSPs). Intermediate bar lengths may produce an average (DC) membrane potential little different from that of the un-stimulated

neuron (figure 4 middle traces). Since action potential generation is a stochastic phenomenon, however, occasional action potentials are still elicited as one or two discrete EPSPs sum temporarily to drive the neuron above threshold.

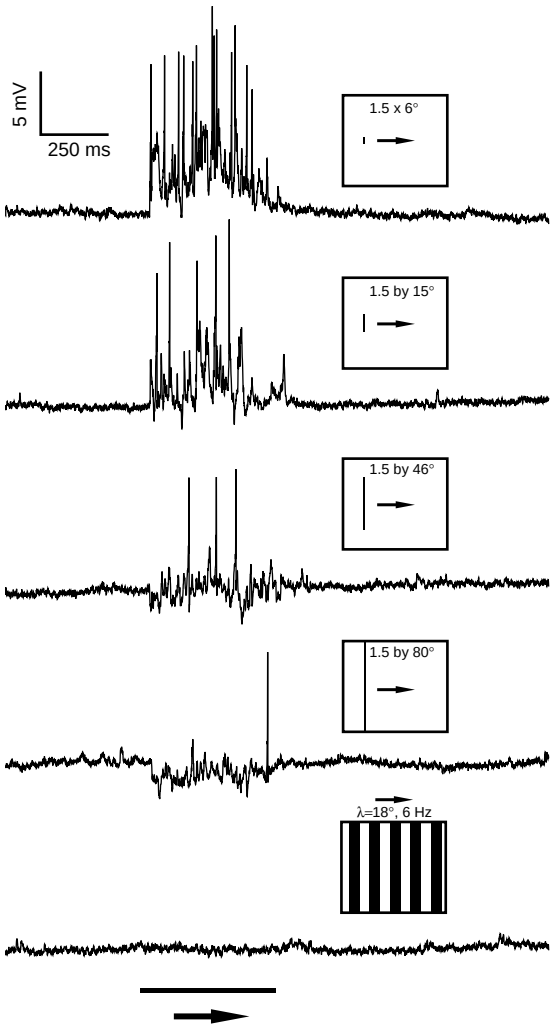

Figure 4. Raw responses recorded intracellularly from an STMD neuron in the lobula of a female hoverfly, *Eristalis tenax* In each trace, a stimulus (as illustrated by each pictogram) was moved across the receptive field of and in the preferred direction of the neuron for the period indicated by the black bar.

If the bar length is increased further, however, the EPSPs are swamped by a summating barrage of IPSPs that may hyperpolarize the neuron by several mV. In this case, the elongated bar clearly inhibits all but the most occasional 'breakthrough' of action potentials elicited by the feedforward excitation. Most interestingly, however, the lower trace in figure 4 shows the response if the moving bar is replaced by a wide-field motion stimulus such as a moving grating pattern. This is a stimulus that would be expected to provide even more powerful inhibition than an elongated bar were the STMDs organized in the manner suggested for FD cells[32,33]. In the case shown, the grating pattern was especially selected to be a

near-optimal stimulus for neurons such as the HS neurons in this species. Yet we see no evidence of *any* post-synaptic 'noise', either excitatory or inhibitory. This suggests the presence of multiple levels of inhibition - in this case at least the addition of a mechanism that inhibits (gates) both excitatory and inhibitory feedforward pathways at a much earlier (presynaptic) level of the system. It is quite possible that the gating signal is itself the output of a 'centrifugal' collator neuron with properties similar to FD neurons or HS neurons.

The simplicity of the experiment illustrated by figure 4 and the wealth of information that such experiments provide underscores the need for many further recordings to elucidate the underlying organization of neurons in this pathway. Ongoing research in my own lab aims to refine basic models for target detection to a point where implementation in neuromorphic hardware is feasible. For example, we are using experiments similar to that in figure 4 to investigate responses to targets moving at different velocities, in the presence of various moving background patterns, and at various locations within the receptive fields of STMDs. These experiments should identify the source of inhibition to 'non-preferred' targets and the effects of pre-synaptic 'gating' of the responses by wide-field stimuli.

Our preliminary data[29,30] are exciting: We find that many small field STMD neurons have a highly asymmetric receptive field organization, with spatially distinct inhibitory and excitatory sub-regions. We are using neuroanatomical staining techniques to identify how this complex receptive field structure is built up, where these neurons receive their inputs, and which cells they target with their outputs. The combination of basic neurophysiological data with modeling in silicon promises to lead to breakthroughs in understanding of these pathways similar to those that have been achieved in the HS system, and, ultimately, to elaborated models of STMDs in silicon.

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