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J. R. Soc. Interface 2004 **1**, 61-77
doi: 10.1098/rsif.2004.0007

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Retinally-generated saccadic suppression of a locust looming-detector neuron: investigations using a robot locust

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A fundamental task performed by many visual systems is to distinguish apparent motion caused by eye movements from real motion occurring within the environment. During saccadic eye movements, this task is achieved by inhibitory signals of central and retinal origin that suppress the output of motion-detecting neurons. To investigate the retinally-generated component of this suppression, we used a computational model of a locust looming-detecting pathway that experiences saccadic suppression. This model received input from the camera of a mobile robot that performed simple saccade-like movements, allowing the model's response to simplified real stimuli to be tested. Retinally-generated saccadic suppression resulted from two inhibitory mechanisms within the looming-detector's input architecture. One mechanism fed inhibition forward through the network, inhibiting the looming-detector's initial response to movement. The second spread inhibition laterally within the network, suppressing the looming-detector's maintained response to movement. These mechanisms prevent a looming-detector model response to whole-field visual stimuli. In the locust, this mechanism of saccadic suppression may operate in addition to centrally-generated suppression. Because lateral inhibition is a common feature of early visual processing in many organisms, we discuss whether the mechanism of retinally-generated saccadic suppression found in the locust looming-detector model may also operate in these species.

Keywords: collision detector; computational model; eye movements; LGMD neuron; DCMD neuron; vision

1. INTRODUCTION

When objects move within an animal's environment, its movement-detecting neurons must respond in order to allow a behavioural reaction to the movement cues. However, when an animal moves its eyes, objects within its visual field also appear to change position although, in reality, they have not moved. Although optomotor neurons must respond to these self-movements (e.g. Hausen 1976; Egelhaaf *et al.* 1989; Krapp & Hengstenberg 1996), neurons detecting small-field object movement must ignore them. During vertebrate eye movements (saccades), these false movement cues are suppressed by saccadic suppression acting on motion-detecting pathways (Zuber & Stark 1966; Burr *et al.* 1994). Saccadic suppression is an important property of both real and artificial eyes and in this paper we investigate how it may be achieved using a computational model of a locust's looming-detecting neurons.

Currently, evidence exists for both a central and retinal mechanism of saccadic suppression. Saccadic suppression may be mediated centrally by a 'corollary

discharge' produced by the saccade generator that cancels saccade-generated motion cues (Sperry 1950; von Holst & Mittelstaedt 1954). Candidate corollary-discharge neurons have been identified in the cat and rabbit (Peck 1984; Lo 1988), as have neurons in primates that are centrally suppressed during saccades (Thiele *et al.* 2002). A locust's descending contralateral movement detector (DCMD) neuron response is also suppressed by a corollary discharge during real and simulated head movements (Zaretsky & Rowell 1979; Zaretsky 1982). In humans, corollary discharge is thought to act early in the visual system within the thalamus or primary visual cortex (Thilo *et al.* 2004).

Saccadic suppression may also be mediated retinally by visual signals generated by the eye's movements (MacKay 1970). This is possible because object movements result in small-field visual stimuli whilst eye movements result in the movement of the whole visual field. Thus the two types of movement may be distinguished using purely visual cues. In humans, a high contrast grating moving in peripheral retina reduces visual sensitivity to a low spatial frequency grating presented at the fovea (Derrington 1984). Furthermore, identified

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neurons in cats show a depression in excitability during saccade-like image movements without accompanying eye movements (Noda 1975) as does the DCMD neuron of a locust (e.g. Zaretsky 1982). An additional hypothesis is that saccadic suppression may not be an active process at all but may result from a mechanical disturbance of the retina resulting from the saccadic eye movement itself (Castet *et al.* 2001).

Locusts possess a pair of uniquely identifiable motion-detecting visual interneurons called the lobula giant movement detectors (LGMDs) (O'Shea & Williams 1974). The LGMDs synapse with a second pair of identified neurons, the DCMDs, that descend to the thorax and may mediate evasive behaviours (Burrows & Rowell 1973; O'Shea *et al.* 1974; Simmons 1980; Rind 1984). The LGMDs and DCMDs respond best to small objects, such as predators or swarm mates, looming towards the locust (Schlotterer 1977; Rind & Simmons 1992) due to the arrangement of the LGMD's afferents from the compound eye (Simmons & Rind 1992). The LGMD's afferents are retinotopically arranged into parallel processing channels and make lateral inhibitory connections that allow excited channels to inhibit their neighbours (O'Shea & Rowell 1975; Pinter 1977; Rowell *et al.* 1977; Pinter 1979; Rind & Simmons 1998). The LGMD is also directly inhibited by a feed-forward pathway from the distal optic lobe that is activated by rapid whole-field image movements and elicits inhibitory postsynaptic potentials (IPSPs) in the LGMD (Palka 1967). A computational model mimicking the LGMD's input architecture has shown that these afferents enable it to respond to looming rather than receding or translating visual stimuli and thus detect potential collisions with objects or predators (Rind & Bramwell 1996). Due to the effectiveness of this LGMD model as a visual collision detector, it has been incorporated into the control structure of a mobile robot, allowing the robot to process visual input from an onboard camera and avoid potential collisions (Blanchard *et al.* 1999; Blanchard *et al.* 2000; Blanchard *et al.* 2001). Subsequently this model has been found to show some of the more sophisticated properties of the locust LGMD neuron, such as the ability to distinguish objects approaching on collision from near-miss trajectories (Judge & Rind 1997; Rind *et al.* 2003).

Because the LGMD neuron of a locust and the model LGMD neuron of a robot respond to small-field movement cues and elicit avoidance behaviour, it is crucial that they are not falsely excited during self movements, i.e. they must be saccadically suppressed. Although a locust cannot produce 'saccades' (because its eyes are fixed to the head capsule), it does produce saccade-like head movements (Kien & Land 1978). Locusts also experience flight deviations that induce similar whole-field image movements. The real LGMDs and DCMDs do not respond during such whole-field movements and are suppressed during real and simulated saccade-like head movements (Rowell *et al.* 1977; Zaretsky & Rowell 1979; Zaretsky 1982). This suppression involves centrally- and retinally-generated components (Zaretsky 1982), with the logarithmically transformed response of the DCMD to a small-field

stimulus reduced by 0.94 log units by corollary discharge resulting from a head movement, and by 0.45 log units as a result of retinally-generated mechanisms (Zaretsky 1982). However, the exact mechanisms involved are unclear. Because the LGMD model incorporates the known connection types presynaptic to the locust LGMD, it allows their role in the retinal component of saccadic suppression to be assessed. In this paper we do this by examining the LGMD model's response to a whole-field stimulus as the different components of inhibition are eliminated in turn, revealing their effect. Our results allow a component of saccadic suppression in the locust to be understood and a mechanism of saccadic suppression for a real-world collision detector to be developed. Because centrally-generated saccadic suppression by corollary discharge has not been fully characterized, it is not represented in the current LGMD model or investigated in this paper.

We found that lateral and feed-forward inhibition comprised a complete system of retinally-generated saccadic suppression in the LGMD model. This was suggested previously (O'Shea & Rowell 1975; Rowell *et al.* 1977) but was not proven experimentally because studying the LGMD's many afferents *en masse* and *in vivo* is very difficult. The presence of this inhibition allows the model LGMD to detect potential collision but not respond during the robot's own turning and translating movements. Due to the presence of lateral inhibition in both the locust LGMD and many vertebrate visual systems, our results may help explain retinally-generated saccadic suppression in higher organisms. Our results also show that the LGMD model can respond in a locust LGMD-like way to simplified real visual stimuli. Such findings may aid in the development of the LGMD model for real-world collision-detection applications.

2. MATERIALS AND METHODS

In this paper we use an LGMD model that incorporates all available evidence on the locust LGMD's input architecture and has been used as a collision detector in a mobile robot by processing visual input from the robot's onboard camera (Blanchard *et al.* 2000). Because the model is tuned to function in a 'real' environment with near-to-natural shadow and illumination conditions, we use simplified real visual stimuli in our experiments. These stimuli were highly structured, allowing the LGMD's response to them to be understood, but were also naturalistic in that they were subject to changing lighting, shadow and contrast conditions. This allows us to investigate the response of the LGMD model to simplified but realistic stimuli, including those that the robot would experience in collision-avoidance applications, without the limitations and predictability imposed by the use of computer-generated stimuli. It also allows us to challenge the model with similar stimuli to those used in experiments on the locust (e.g. Rowell *et al.* 1977; Zaretsky & Rowell 1979; Zaretsky 1982). This section outlines the processing in the LGMD model, from visual input to an LGMD response, and the specific experiments undertaken.

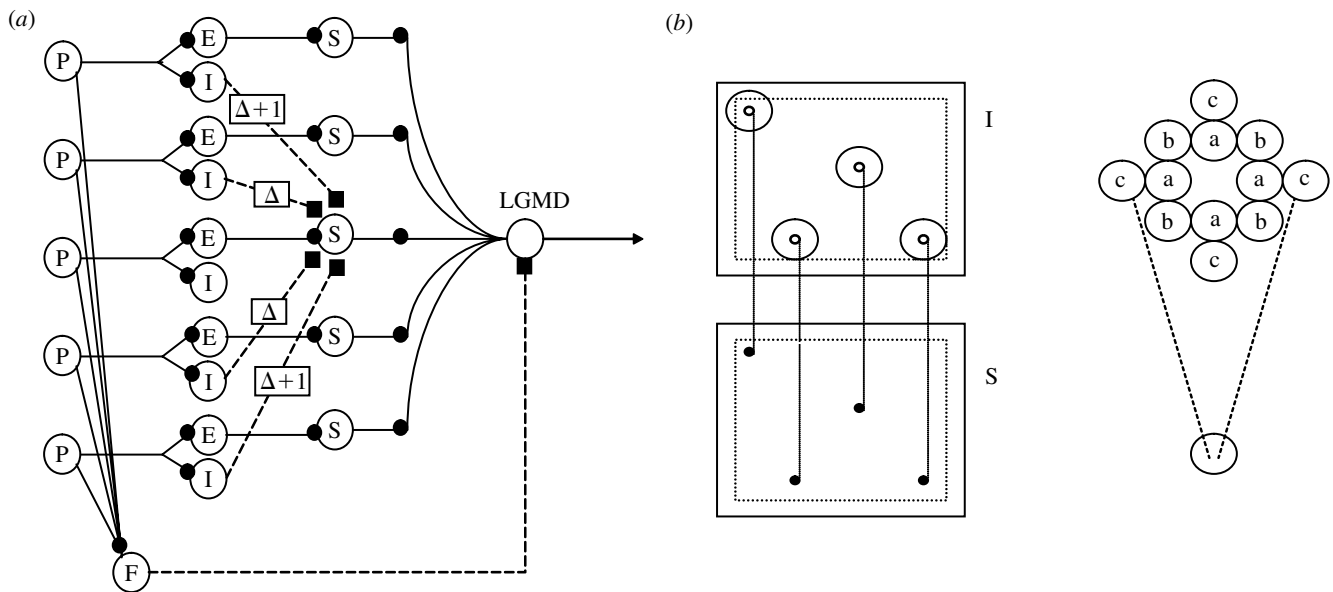


Figure 1. (a) A schematic of the structure of the LGMD model used in simulation experiments. Excitatory connections are indicated by solid lines and filled circles, inhibitory connections are indicated by dashed lines and filled squares. Visual input was received by P-cells in layer 1 which excited E- and I-cells in layer 2. The E-cells passed direct retinotopic excitation whilst the I-cells passed lateral inhibition. These signals were summed by S-cells in layer 3 which in turn excited the LGMD-cell. Feed-forward inhibition was mediated by the F-cell which inhibits the LGMD-cell when excited by a sufficient number of simultaneously excited P-cells. (b) Explanation of connections between the I and S groups in the LGMD model (see table 2). Each of the central 1296 cells in the S group was connected to a ring of 12 retinotopically surrounding cells in the I group to create lateral inhibition. The remaining cells in the peripheral area of the S group (denoted by the dotted line) were not connected. Synaptic weights and delays were set according to the positions of pre- and postsynaptic cells. The strength and delay parameters used were: a, strength = 0.17, delay = 1; b, strength = 0.12, delay = 1; c, strength = 0.08, delay = 2 (diagram modified from Blanchard *et al.* 2000).

2.1. Visual processing in the LGMD model

Visual input to the LGMD model was from the K2D-B/W-PAL video turret of a Khepera mobile robot (K team, Lausanne, Switzerland). This turret incorporates a miniature CCD camera with a resolution of 500(H) $\times$ 582(V) pixels and a 5 mm (F 3.6, 68.8°(H) $\times$ 48.5°(V)) lens. Images from this camera were captured using a Hauppauge WinTV card fitted in a desktop PC with an Intel Pentium III 866 MHz processor and 256 MB RAM (Dan Technology).

Images were used as visual input to the model LGMD simulation which ran in the neural simulation program IQR₄₂₁ (originally known as Xmorph) on the desktop PC (Verschure 1997). At each simulation timestep (approximately 13 s⁻¹) the image captured at timestep $t - 1$ was subtracted from that captured at timestep t to give an 'absolute difference' image indicating movement in the camera's field of view. This image was mapped onto a square array of 40 $\times$ 40 simulated IQR₄₂₁ cells with non-overlapping but touching, equal sized fields of view. The response of each of these cells was a graded potential according to the amount of movement within its visual field. Filtering images for movement prior to the absolute difference group mimicked the response dynamics of insect photoreceptors with a transient, adapting response to novel movement (e.g. Laughlin 1981).

Signals from the 'absolute difference' cell group were used as input to layer 1 of the 4 layer LGMD simulation.

Each layer of the simulation was a 40 $\times$ 40 square grid of simulated cells (figure 1a) and the activity of each of these cells was calculated at each timestep according to the cell's type. Layer 1 of the model was composed of P-cells, which represented the first layer of visual processing in the locust eye—the photoreceptors. P-cells were modelled as 'integrate and fire' cells and the membrane potential of a cell i , $v_i(t + 1)$, at each timestep was calculated by

$$v_i(t + 1) = VmPrs_i v_i(t) + ExGain_i \sum_{j=1}^m w_{ij} a_j(t - \delta_{ij}) - InhGain_i \sum_{k=1}^n w_{ik} a_k(t - \delta_{ik}), \quad (2.1)$$

where $v_i(t)$ is the cell's membrane potential from the previous timestep, $VmPrs_i$ is the persistence of the membrane potential, $ExGain_i$ and $InhGain_i$ are the gains of excitatory and inhibitory inputs respectively, m is the number of excitatory inputs, n is the number of inhibitory inputs, w_{ij} and w_{ik} are the strengths of the synaptic connections between cells i and j and i and k respectively, a_j and a_k are the output activities of cells j and k , and $\delta_{ij} \geq 0$ and $\delta_{ik} \geq 0$ are the delays along the connections between cells i and j and i and k (tables 1 and 2) (Blanchard 1999; Blanchard *et al.* 2000). From this membrane potential the output activity of these

Table 1. IQR₄₂₁ cell parameters used for the calculation of membrane potential and activity for each cell type used in the LGMD model. Parameters are described in the text and apply to equations (2.1)–(2.3). All parameters are given in the arbitrary units used by the IQR₄₂₁ simulation software.

Name	Type	ExGain	InhGain	Thres	Slope	VmPers
P-cell	I&F	—	—	0.05	1	0.4
E-cell	LinTh	0.6	0	0.00	—	0.1
I-cell	LinTh	0.2	0	0.00	—	0.8
S-cell	I&F	1.0	1	0.50	1	0.4
F-cell	LinTh	0.2	0	0.15	—	0.1
LGMD-cell	I&F	2.0	5	0.25	1	0.4

Table 2. IQR₄₂₁ synapse parameters used in the LGMD simulation. These apply to equations (2.1)–(2.3). Synapse type is indicated by + (excitatory) or – (inhibitory) and *Npre* and *Npost* describe the number of presynaptic and postsynaptic cells respectively. *Strength* (*w*) is given in IQR₄₂₁ units and *Delay* (δ) is given in IQR₄₂₁ timesteps.

Synapse	Type	Arborization	<i>Npre</i>	<i>Npost</i>	<i>Strength</i> (<i>w</i>)	<i>Delay</i> (δ)
P-to-E	+	1:1	1600	1600	1.00	0
P-to-I	+	1:1	1600	1600	1.00	0
E-to-S	+	1:1	1600	1600	1.00	0
I-to-S	–		(see figure 1 <i>b</i>)			
S-to-LGMD	+	1296:1	1296	1	0.04	0
P-to-F	+	1600:1	1600	1	0.04	0
F-to-LGMD	–	1:1	1	1	1.00	1

cells ($a_i(t+1)$, a spike) was calculated by

$$a_i(t+1) = \begin{cases} \text{Slope,} & \text{with probability Prob} \\ & \text{for } v_i(t+1) \geq \text{ThSet,} \\ 0, & \text{otherwise,} \end{cases} \quad (2.2)$$

where *Slope* is the amplitude of output spikes, *ThSet* is the membrane potential of the cell and *Prob* is the probability of spiking activity (table 1) (Blanchard 1999; Blanchard *et al.* 2000). Due to the arrangement of the P-cells in a 40×40 grid, each P-cell had an acceptance angle of 1.72° in the horizontal plane which compared favourably with the acceptance angle of $1.5 \pm 0.2^\circ$ measured for light-adapted locust photoreceptors (Wilson 1975), matching the LGMD model's spatial resolution to that of the locust. Unlike insect photoreceptors which do not produce spikes (e.g. Laughlin 1981), each P-cell in the LGMD model produced a spike in response to edges crossing its field of view. However, in conjunction with the absolute difference cell group, the P-cells produced a brief and transient response to image movement that mimicked the rapidly adapting properties of insect photoreceptors to sustained stimulation (e.g. Laughlin 1981) and the similar, transient response properties of other neurons in the medulla of the locust's optic lobe which receive input from the photoreceptors and may be input to the LGMD (Osorio 1986; Osorio 1991; James & Osorio 1996). The absolute difference and P-cells must therefore be thought of as a composite of these cell types.

P-cells passed excitation retinotopically to 40×40 square grids of excitatory E-cells and inhibitory I-cells and a single feed-forward inhibitory F-cell in layer 2. These were all 'linear threshold' cells, meaning that their membrane potentials were calculated from equation (2.1) whilst their output activity ($a_i(t+1)$, a

graded potential) was calculated by

$$a_i(t+1) = \begin{cases} v_i(t+1), & \text{with probability Prob} \\ & \text{for } v_i(t+1) \geq \text{ThSet,} \\ 0, & \text{otherwise,} \end{cases} \quad (2.3)$$

where *ThSet* is the membrane potential threshold and *Prob* is the probability of activity (tables 1 and 2) (Blanchard 1999; Blanchard *et al.* 2000). The E(excitatory)- and I(inhibitory)-cells passed excitation and inhibition respectively to layer 3 of the simulation. This was a 40×40 square grid of integrate and fire S-cells (summing cells) whose membrane potential and output activity was calculated from equations (2.1) and (2.2) (tables 1 and 2). Each S-cell received excitation from the single E-cell in the same retinotopic position as itself in layer 2. It also received inhibition from I-cells in neighbouring and next-neighbouring retinotopic positions in layer 2 (figure 1*b*). This represented the lateral inhibition present presynaptic to the locust LGMD (O'Shea & Rowell 1975; Pinter 1977; Rowell *et al.* 1977; Pinter 1979; Rind & Simmons 1998). However, the temporal properties of these inhibitory connections were obtained from tuning the model to detect looming stimuli due to the slower temporal frequency of the network's P-cells (13 frames s^{-1}) compared to the flicker fusion frequency of the locust's photoreceptors (54 Hz for *L. migratoria* (Carricaburu & Duhaze 1978)). The response of the model LGMD to a looming stimulus has previously been directly compared to that of the locust LGMD, revealing a tight similarity in their responses (Rind & Bramwell 1996). Because S-cells on the edge of the array could not receive lateral inhibition from all sides, only the central 1296 S-cells were used in the simulation. These S-cells summed excitatory and inhibitory input and their output was conveyed to layer 4 of the network.

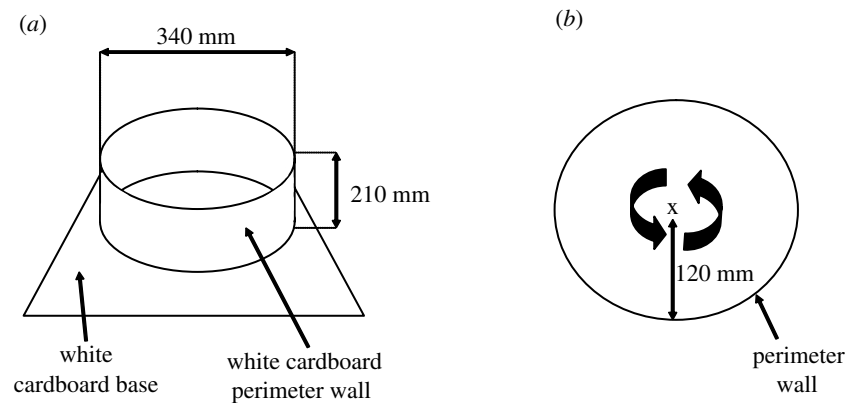


Figure 2. The experimental arena used in our experiments to deliver real whole-field grating stimuli to a Khepera mobile robot. These stimuli were similar to those used in experiments on the locust and represent the types of stimuli the LGMD model faces in real-world collision-detection applications. (a) The dimensions of the experimental arena. (b) The position of the Khepera robot during rotation within the experimental arena.

The single F-cell in layer 2 received excitation from each P-cell in layer 1 but bypassed layer 3 to transfer a single inhibitory output to layer 4 of the network. This represented the feed-forward inhibition experienced by the locust LGMD neuron (Palka 1967) and, as with lateral inhibition, its temporal properties were obtained from tuning the network to detect looming stimuli (Rind & Bramwell 1996).

Layer 4 of the simulation comprised a single integrate and fire LGMD-cell that received excitatory input from the central 1296 S-cells in layer 3 and inhibitory input from the single F-cell in layer 2 (tables 1 and 2). These inputs were summed to give a membrane potential and spiking activity using equations (2.1) and (2.2). In previous experiments this spiking activity was used to elicit avoidance reactions (Blanchard *et al.* 2000; Blanchard *et al.* 2001) but in our experiments it was recorded and had no effect on the robot's movement.

2.2. Stimulating the network with simplified real looming and whole-field visual stimuli

In order to confirm the LGMD model's response to a looming stimulus, the robot was made to approach an 80 mm diameter black sphere at a speed of 25 mm s^{-1} . This approach was over a distance of 1800 mm along a direct collision trajectory within a featureless white arena. In order to challenge the robot with wide-field visual stimuli we constructed a simple experimental arena. This was an open topped drum measuring 210 mm in height and 340 mm in diameter (figure 2). We fixed sinusoidal grating stimuli, single stripe stimuli with sinusoidal intensity profiles or two sinusoidal intensity stripes at varying angular separations to the inside wall of this drum. All stimuli were created using Micrographics Draw. We placed the robot in the centre of the drum and, due to the position at which the robot's camera was mounted on its wheelbase, the distance between the CCD camera lens and the arena wall was constant at 120 mm. In each experiment we instructed the robot to rotate within its arena using the Linux Minicom terminal emulator. In all of our experiments the robot rotated at $53.7^\circ \text{ s}^{-1}$ which corresponds to

approximately 4.1° per IQR₄₂₁ timestep. This speed is slower than the mean velocity of a locust's saccadic head movements (140° s^{-1} ; Kien & Land 1978) but was a common saccadic stimulus experienced by the model LGMD in the collision detection applications for which it was developed (Blanchard *et al.* 2000).

We recorded the LGMD network's response to whole-field stimuli with various elements of its input architecture removed in order to investigate their role. We removed lateral inhibitory and feed-forward inhibitory connections using the IQR₄₂₁ graphical user interface. We also removed the persistence of lateral inhibition by reducing the membrane potential persistence of the I-cells, meaning that their membrane potential could only reach threshold whilst directly excited, preventing lateral inhibition from being conveyed for a sustained period after a visual stimulus had excited the I-cell. We also reduced the ability of this inhibition to persist at the S-cells so that these would only be affected by direct inhibition and not by the persisting effects of inhibition after input from the I-cell had ceased. We recorded the excitation and activity of the simulated LGMD-cell using the IQR₄₂₁ analysis tool. Excitation, recorded as the total amount of excitation delivered to the LGMD-cell from all S-cells, could be affected by lateral and not feed-forward inhibition. LGMD activity, measured as spikes, could be affected by both types of inhibition and was previously used as the avoidance-eliciting output of the model in robotic experiments (Blanchard *et al.* 2000). This allowed us to assess the respective contributions of lateral and feed-forward inhibition to suppression of the behaviourally relevant LGMD response.

We also recorded the model LGMD's response under a simple test scenario which represented the visual processing task for which the model LGMD was designed—looming detection. In this experiment the robot first translated, then rotated and approached a spherical stimulus on a collision course, all within a structured environment (refer ahead to figure 11 for a diagram). Due to the more complex course of the robot in this experiment it was controlled by a simple program written in Matlab (Mathworks Inc, USA) and running on an

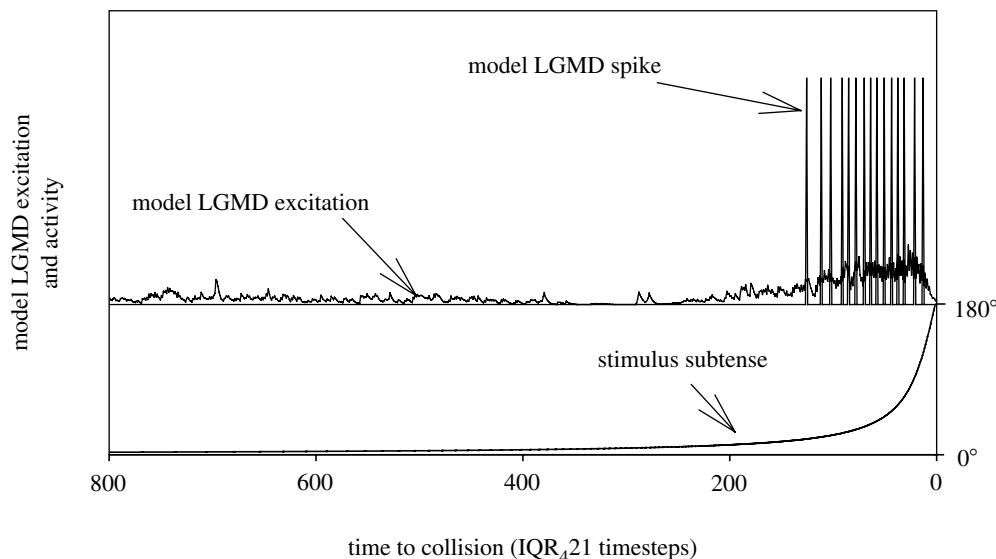


Figure 3. The response of the model LGMD during a direct approach towards an 80 mm diameter black sphere at 25 mm s^{-1} over a distance of 1800 mm. The LGMD model produces a train of spikes which increase in frequency as time to collision approaches, giving a warning of impending collision. Model LGMD excitation and activity both decline prior to collision as a result of feed-forward inhibition and the edges of the looming object leaving the camera's field of view. Top plot: the jagged trace indicates excitation delivered to the model LGMD and vertical lines indicate spiking activity in the model LGMD. Lower plot: the calculated subtense of the looming sphere on the robot's camera.

Ergo Elite II laptop with an Intel Pentium III 600 MHz processor and 256 MB RAM (Ergo computing). Camera input from the robot was fed to the LGMD model running on the desktop PC as before which, due to the reduced processing occurring on the PC, ran at $25 \text{ timesteps s}^{-1}$. Data from these trials were captured as for the previous experiments.

We exported the captured data to SigmaPlot 2000 for Windows where we plotted it against each step of simulated time. Our unpublished data show very little variation in the model LGMD's response under controlled conditions (Santer and Rind, unpublished observations) and thus a single stimulus presentation was sufficient for many of the experiments presented in this paper.

Data from experiments testing two conditions of lateral inhibition using two bar stimuli at varying angular separations were analysed using a two-way ANOVA test to assess any interaction between the effects of lateral inhibitory condition and the effects of varying bar separation. A *post hoc* Tukey test was then used to determine which angular bar separations resulted in a significant lateral inhibitory effect. These analyses were performed using MINITAB statistical software.

3. RESULTS

3.1. Model LGMD responses to looming stimuli

Initially we investigated the response of a previously described and biologically authentic LGMD model (Rind & Bramwell 1996; Blanchard *et al.* 2000), which received visual input from the camera of a mobile robot, during the robot's approaches towards an 80 mm diameter black sphere stimulus. During such approaches the model produced a locust LGMD-like train of spikes which increased in frequency as the time to collision

decreased (e.g. Schlotterer 1977; Rind & Simmons 1992; Gabbiani *et al.* 1999), thus giving a warning of impending collision (figure 3). This is supported by previous experiments where this response has been directly compared to that of the locust LGMD (Rind & Bramwell 1996), and where it has been used to help a mobile robot to avoid potential collisions (Blanchard *et al.* 2000).

3.2. Model LGMD responses to simplified whole-field stimuli

We next analysed the LGMD model response to real, whole-field grating stimuli. The response of the locust LGMD neuron is suppressed by these stimuli (e.g. Palka 1967; O'Shea & Rowell 1975; Rowell *et al.* 1977) and we wanted to ascertain whether the LGMD model response could also be suppressed in the same way, preventing a false collision warning signal. Initially we tested the response of the complete LGMD model to a whole-field grating with a 4° stripe period moving at 4.1° per step of simulated time (contrast frequency 1.0° per timestep) (figure 4a). This stimulus did not strongly excite the model LGMD. As grating movement began, excitation delivered to the model LGMD from its excited afferents peaked and a single spike was initiated in the simulated cell. However, as grating movement continued, excitation delivered to the model LGMD was quickly cut back and spiking activity ceased. Thus the LGMD model showed retinally-generated suppression of its response to whole-field stimuli. This is a similar pattern of response to that shown by the locust LGMD, which responds to low contrast frequency whole-field drifting gratings with an initial burst of spikes (three in response to $\text{CF} = 3 \text{ Hz}$) which are rapidly suppressed as grating movement continues (Rowell *et al.* 1977).

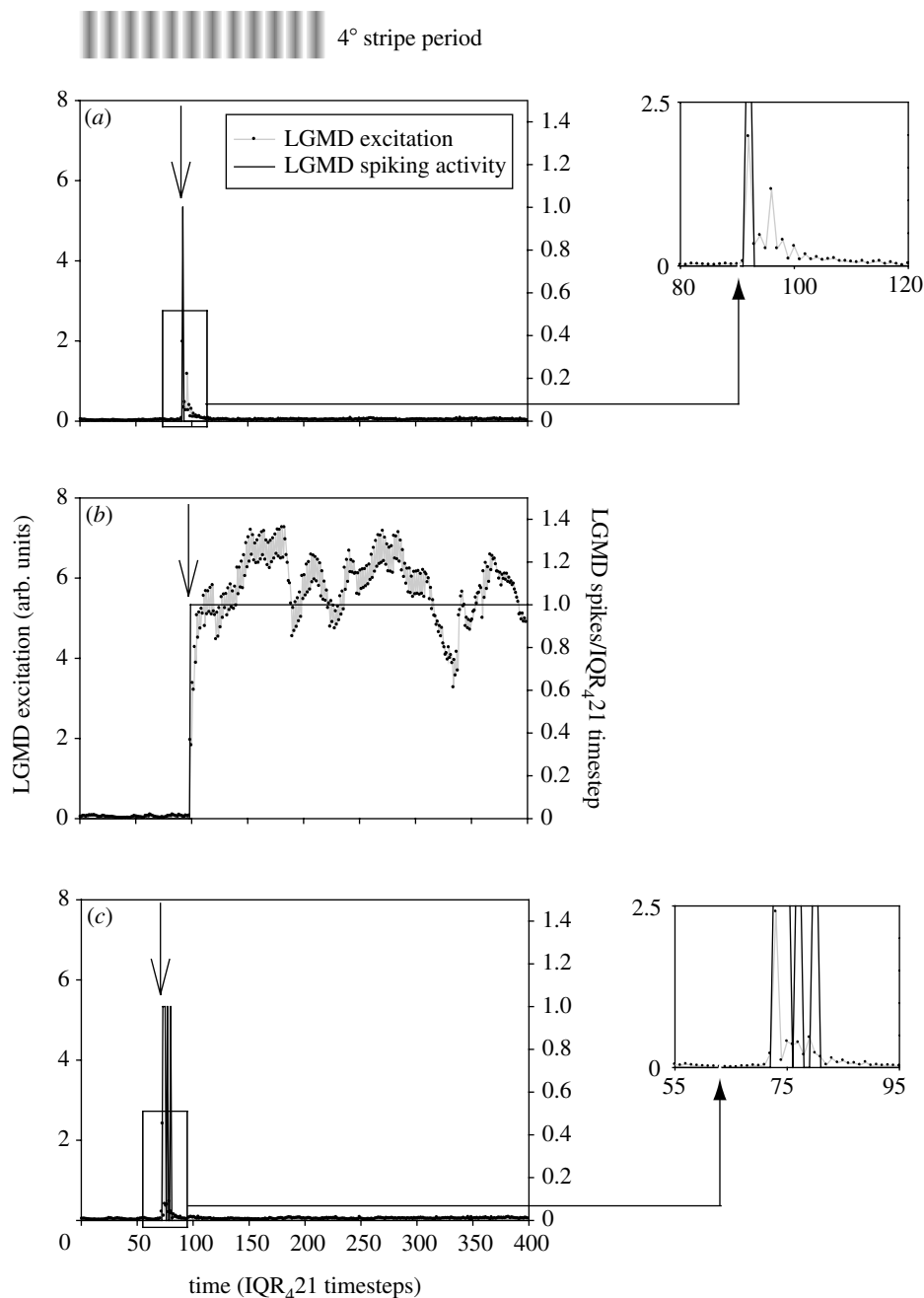


Figure 4. The response of the model LGMD neuron to the rotation of a drifting grating with a 4° stripe period. The solid black line in each graph indicates the spiking activity of the model LGMD whilst the dotted grey line indicates the excitation that it receives. As lateral inhibition acts presynaptic to the model LGMD, it will effect the excitation received by the model LGMD neuron. The model LGMD's spiking activity will be affected by both lateral and feed-forward inhibition. Each plot shows data from a single stimulus presentation. (a) In the complete model a brief LGMD response was elicited as whole-field stimulus movement began (arrow). This was quickly cut back and the model LGMD response was suppressed as grating movement continued (see inset). (b) When lateral inhibitory connections were removed from the LGMD model, it responded powerfully to movements of a drifting grating stimulus and its response was not suppressed as stimulus movement continued. In this trial excitation delivered to the model LGMD was variable. (c) When feed-forward inhibitory connections were removed from the original LGMD model it responded powerfully to the onset of grating movement with several spikes. However, its response to sustained grating movement was still suppressed and the excitation it received followed a similar profile to that shown by the intact LGMD model (inset).

In the locust, these stimuli result in no IPSPs in the LGMD from feed-forward inhibition whilst higher contrast frequencies do, removing the initial LGMD spikes in response to these stimuli (Rowell *et al.* 1977).

Having shown that the LGMD model responded in a locust LGMD-like way to whole-field stimuli, we

next investigated the mechanism of retinally-mediated LGMD response suppression. By using a computational model rather than an electrophysiological investigation of the locust itself, we were able to investigate the role of lateral inhibition in saccadic suppression of the LGMD response by removing all lateral inhibitory connections

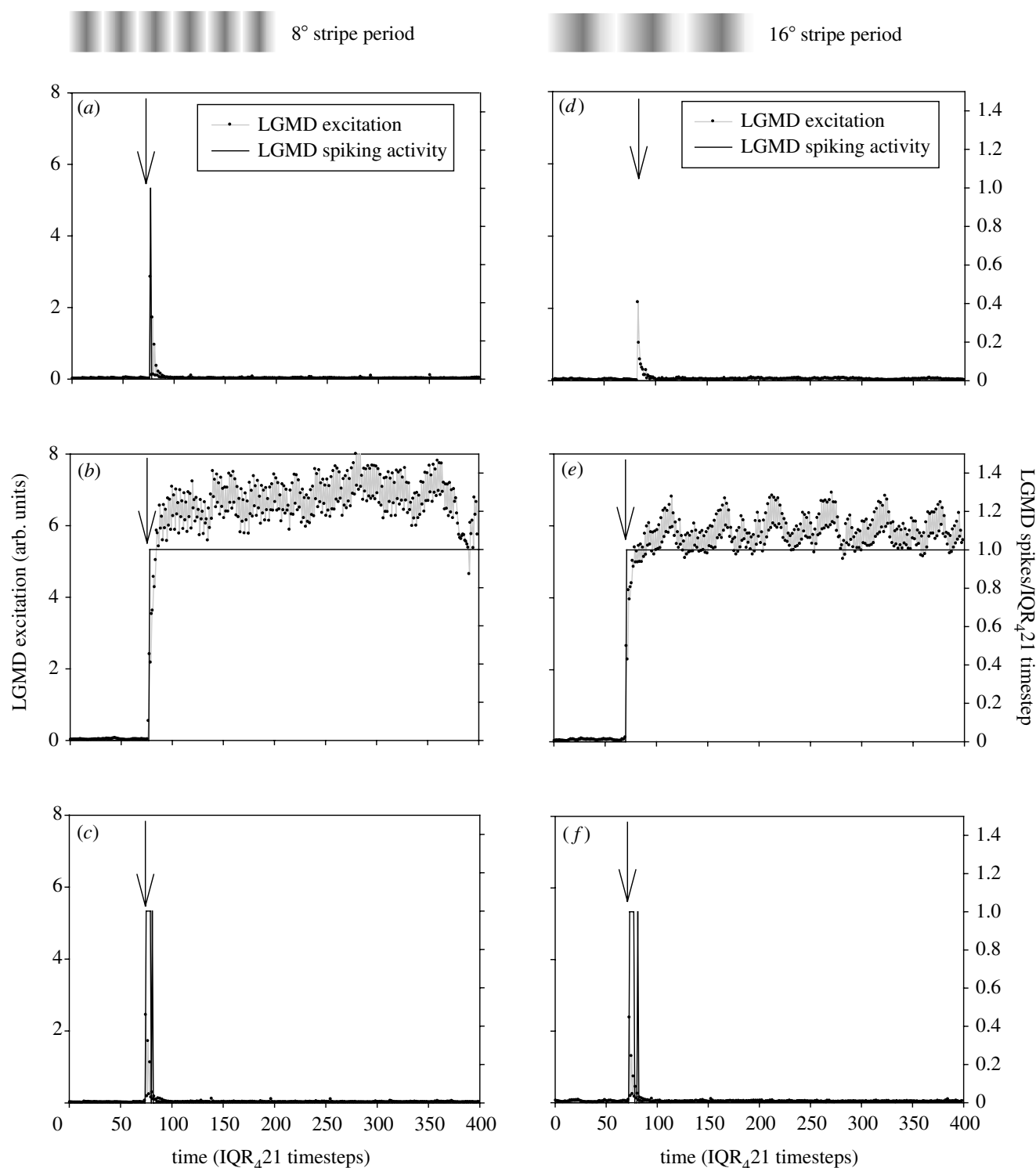


Figure 5. The response of the model LGMD neuron to 8° ((a), (b) and (c)) and 16° ((d), (e) and (f)) stripe period gratings traversing its field of view. In both cases the intact model LGMD responded briefly to the onset of grating movement, after which its response was suppressed ((a) and (d)). With lateral inhibition removed from the model it responded powerfully throughout grating movement with a variable excitation profile and constant spiking activity ((b) and (e)) and with feed-forward inhibition removed it responded strongly to the onset of grating movement before its response was suppressed as movement continued ((c) and (f)). Data are from a single presentation of each stimulus.

from the LGMD model and re-testing its response to the same whole-field stimulus used in the previous experiment (figure 4b). With lateral inhibitory connections removed, the LGMD model responded strongly to the drifting grating stimulus. As grating movement began,

excitation to the model LGMD was powerful and did not decrement throughout stimulus presentation. As a result, during grating rotation the model LGMD began to spike and continued to do so at each step of simulated time. This is in agreement with recordings from the

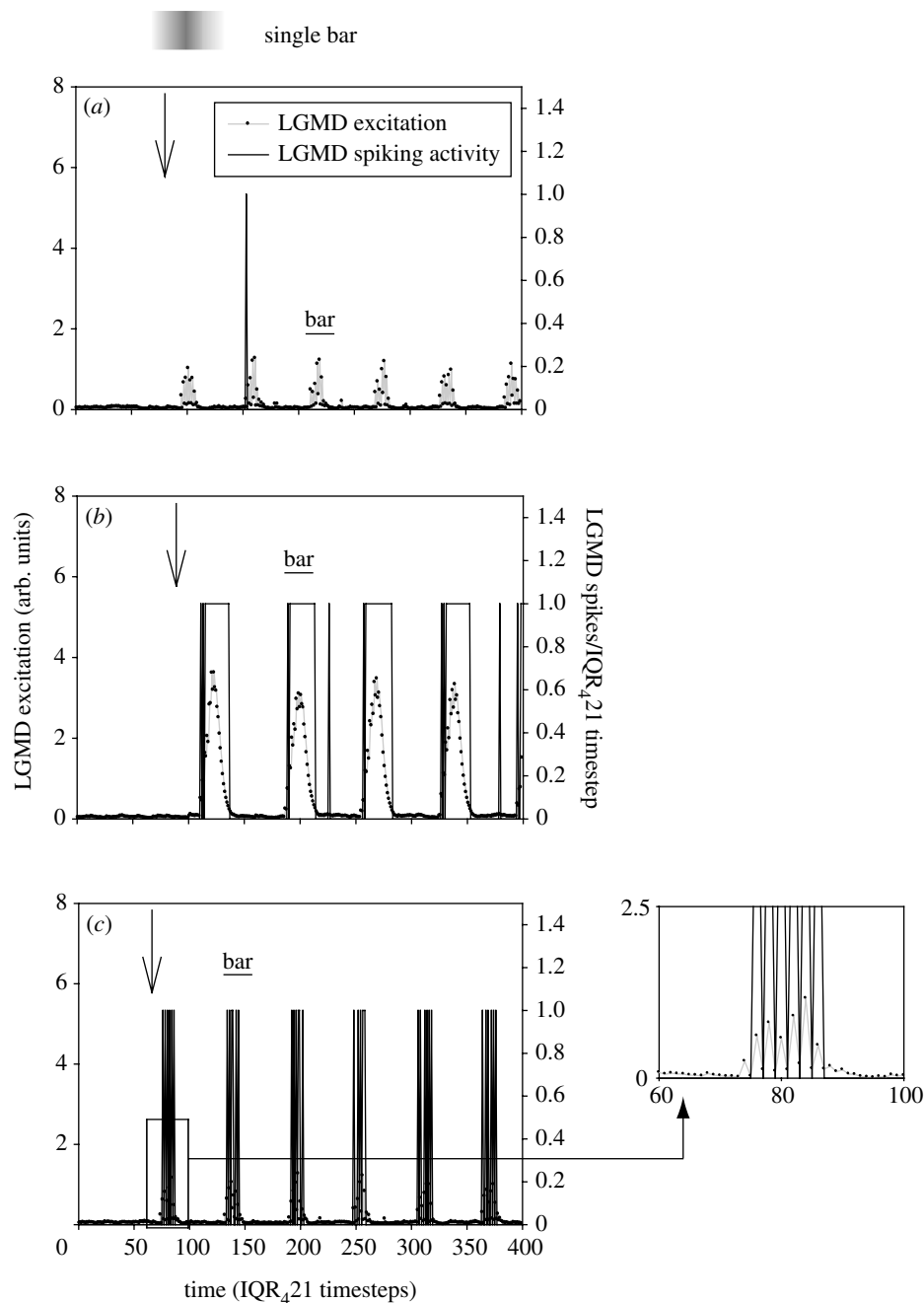


Figure 6. The LGMD model response to a single bar stimulus (23.54° subtense, sinusoidal intensity profile) traversing its field of view. The bar was visible within the field of view for approximately 23 timesteps on each stimulus pass (one example pass is indicated by a line labelled 'bar' on each plot) and each plot is from a single stimulus presentation. (a) The intact LGMD model received a small amount of excitation each time the bar stimulus traversed its field of view. Each above baseline excitation profile represents the passage of the bar across the camera's field of view. The bar's movement only occasionally resulted in a single model LGMD spike. (b) With lateral inhibition removed, the LGMD responded powerfully during and after the time that the bar was visible within the camera's field of view (LGMD response duration of 26 timesteps). During each stimulus pass the model LGMD received more excitation than was evident in the intact model and produced constant spiking activity. (c) When feed-forward inhibition was removed, the model LGMD responded with a burst of spikes each time the bar appeared within its field of view. This response was weaker and of shorter duration (12 timesteps) than the response of the LGMD model with lateral inhibitory connections removed and was not sustained throughout the time that the bar was visible within the camera's field of view. Inset shows detail of excitation and inhibition during one stimulus pass so that the excitation profile can be clearly seen.

locust LGMD which suggest that lateral inhibition removes these spikes from its response to a drifting grating (Rowell *et al.* 1977).

In addition to lateral inhibition, feed-forward inhibition, impinging directly onto the LGMD from the

locust's distal optic lobe, may play a role in suppressing an LGMD response to whole-field stimulation. This is suggested from locust LGMD recordings where no feed-forward IPSPs result from the presentation of low contrast frequency gratings, resulting in a burst of

LGMD spikes at the onset of stimulus movement, whilst IPSPs do result from high contrast frequency gratings removing the initial spikes from the LGMD response (Rowell *et al.* 1977). We investigated this possibility by re-instating lateral inhibitory connections and removing feed-forward inhibition from the LGMD model before re-testing its response to whole-field stimulation (figure 4c). In this trial, excitation delivered to the model LGMD initially peaked and followed a similar profile to that observed in the intact model (compare insets in figures 4a and 4c). However, in the absence of feed-forward inhibition, a burst of 4 model LGMD spikes was generated. As grating movement continued, excitation to the model LGMD was cut back and spiking activity ceased.

We repeated these experiments with 8° (contrast frequency 0.51° per timestep) and 16° (contrast frequency 0.25° per timestep) stripe period sinusoidal gratings in order to observe the effects of the spatial frequency of the whole-field stimuli on the degree of model LGMD response suppression (figure 5). In the locust, lower contrast frequency gratings elicit a larger burst of initial spikes in the LGMD because feed-forward inhibition is not activated (Rowell *et al.* 1977). However, these stimuli both elicited a similar response in the model LGMD to that of the 4° drifting whole-field grating both in the presence or absence of lateral- or feed-forward inhibition. Both gratings elicited feed-forward inhibition in the model LGMD neuron, unlike in the locust LGMD where low contrast frequency gratings do not (Rowell *et al.* 1977).

3.3. The mechanism of model LGMD response suppression by lateral inhibition

We tested the LGMD model response to a single 23.54° subtense bar traversing its field of view at 4.1° per step of simulated time (figure 6). The complete LGMD model responded weakly to this stimulus with a burst of excitation each time the bar crossed the camera's field of view (figure 6a). However, when lateral inhibitory connections were removed the model LGMD now responded strongly each time the bar traversed its field of view (figure 6b). In contrast, when the feed-forward inhibitory connections were removed, the model responded to the appearance of the bar within its field of view but gave a much briefer and weaker response than when lateral inhibitory connections were removed (figure 6c).

Because the intact LGMD model showed a suppressed response when stimulated with a single bar, we concluded that lateral inhibitory connections were not directly mediating antagonism between two stimuli. Instead we hypothesized that lateral inhibition could achieve its effect by spreading in advance of the traversing bar and persisting in areas of soon-to-be-excited retina at the S-cell layer. We used our LGMD model to investigate this by studying its response to two traversing bar stimuli when lateral inhibitory connections were active and when they were removed. We used two 23.54° subtense bars separated by 79.61° or by 102.68° (figure 7). The model LGMD response in terms of excitation induced by the first and second bars crossing

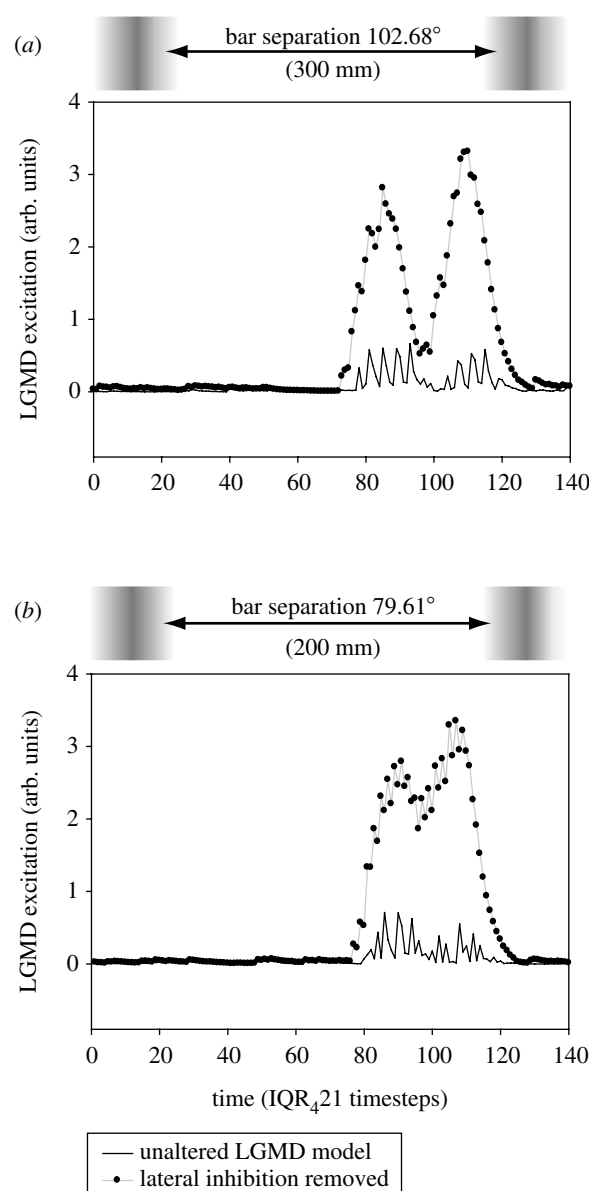


Figure 7. The response of the model LGMD to the passage of two separate 23.54° subtense sinusoidal intensity profile bars across its field of view at bar separations of (a) 102.68° and (b) 79.61° . In each graph an excitation event occurs throughout the time that a bar is visible within the camera's field of view. For smaller bar separations (b), the time between two bars being visible within the field of view is small and thus the two excitation events form a compound waveform. For bar separations of (a) 102.68° and (b) 79.61° the response of the intact LGMD model was less, in terms of excitation received, to the passage of the second bar. However, with lateral inhibitory connections removed, the response of the model LGMD was increased to the passage of the second bar. Data are from a single stimulus presentation.

the camera's field of view was a compound waveform. In the complete model, with lateral inhibitory connections present, the model LGMD response to the second bar was reduced relative to the first as a result of lateral inhibition. This was most notable at the closest bar separation. However, when lateral inhibitory connections were removed, the model LGMD response to the second bar was increased relative to the first. This increase in

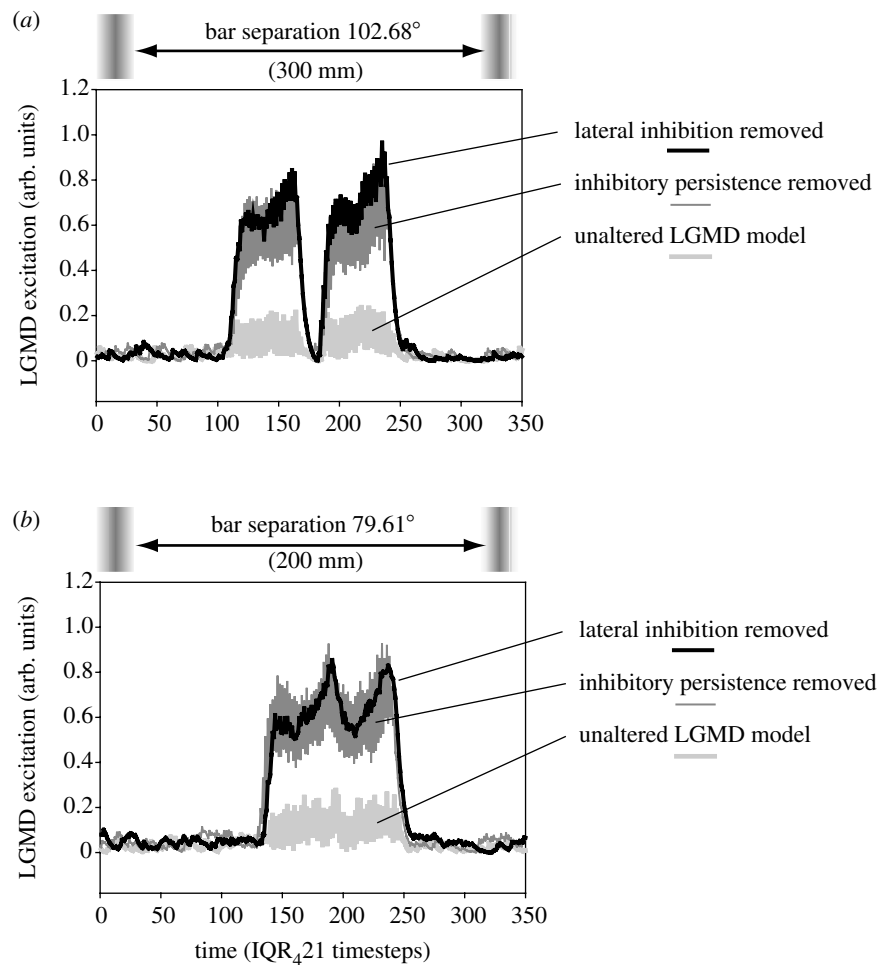


Figure 8. The response of the model LGMD to the passage of two narrow (4.77° subtense) bars across its field of view for the bar separations used in figure 7. In these experiments the removal of lateral inhibitory persistence had the same effect on excitation received by the model LGMD as the removal of lateral inhibitory connections entirely. The response of the unaltered LGMD model is shown for comparison. Data are from a single stimulus presentation.

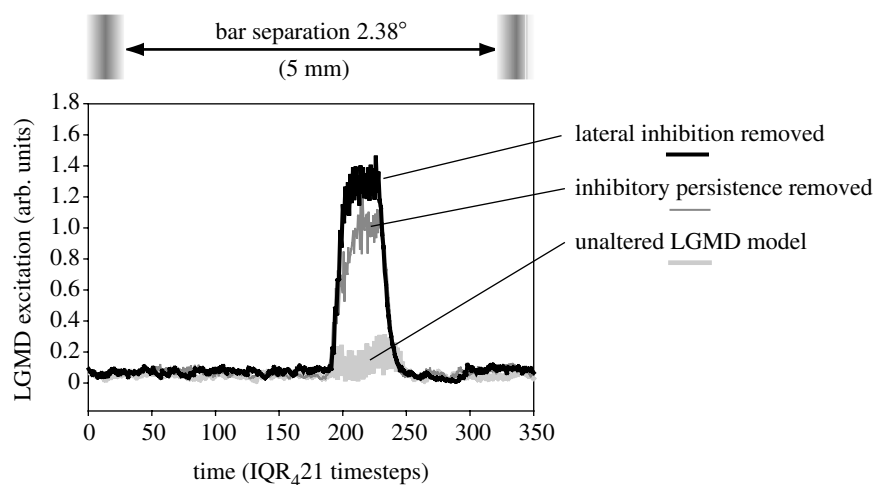


Figure 9. The response of the model LGMD to two narrow (4.77° subtense) bar stimuli crossing its field of view. In this experiment the separation of the two bars was 2.38° . As a result, the separate responses of the model LGMD to the first and second bar cannot be distinguished as both were visible within the camera's field of view simultaneously. For these small bar separations, the removal of lateral inhibitory persistence had a lesser effect than the removal of lateral inhibitory connections entirely. The response of the unaltered LGMD model is shown for comparison. Data are from a single stimulus presentation.

the model LGMD's response resulted from excitation generated by the first bar persisting in the network and being summed with excitation from the second bar as it passed over that area of simulated retina.

Lateral inhibition in the LGMD model could reduce its response to the second of two traversing bars separated by over 79° at the camera (figure 7). In the LGMD model, each photoreceptor had an acceptance angle in the horizontal plane of 1.72° . The maximum extent of each lateral inhibitory connection was to the next neighbouring channel which is 5.16° at the camera. Lateral inhibition was delayed by 1 step of simulated time, during which the robot was able to rotate a further 4.1° . As a result, in order for two bar stimuli to interact directly via active lateral inhibition between simultaneously excited processing channels they may only be separated by a maximum of 9.26° . In our model, lateral inhibition was able to function over a greater distance (figure 7), so the persistence of this inhibitory signal in areas of previously inhibited retina appeared crucial to the effective functioning of lateral inhibition.

We next tested the LGMD model response to two 4.77° subtense bars traversing its field of view at 4.1° per timestep. When these bars were separated by 102.68° or 79.61° the response of the model LGMD with the ability of lateral inhibition to persist removed, was similar to the response of the model with lateral inhibitory connections entirely removed (figure 8). Therefore, in these experiments the persistence of lateral inhibition in the LGMD network was entirely responsible for the suppression of the model LGMD's response to the two traversing bars. In these trials, suppression of the response to the second bar in the intact model was greatly reduced due to the smaller bars inducing less lateral inhibition in the system which did not allow the two bars to interact at large bar separations (figure 8*a*). However, the response to both bars showed the effects of lateral inhibition when compared to the response of the model with no lateral inhibition. This resulted from the LGMD response to each bar being affected by the inhibition that bar had generated. When we tested a smaller bar separation of 2.39° the response of the LGMD model with lateral inhibitory persistence removed was less than the response of the model with lateral inhibitory connections entirely removed (figure 9). In this instance, when the two bars were close enough together to allow inhibition to interact directly between simultaneously active processing channels, direct interactions also contributed to the suppression of the LGMD response to the second bar stimulus. We did not observe this effect for very small bar separations less than the acceptance angle of a single P-cell (bar separation 1.19°) (figure 10). A two-way ANOVA test showed a significant interaction between bar separation (a fixed factor) and lateral inhibitory condition (lateral inhibitory connections removed or lateral inhibitory persistence removed but connections intact, a fixed factor) ($F_{6,319} = 6.05$, $P < 0.001$). A *post hoc* Tukey test showed a significant difference ($P < 0.05$) between the response of the model with lateral inhibition removed and the response of the model with lateral inhibitory persistence removed but lateral inhibitory connections intact at bar separations

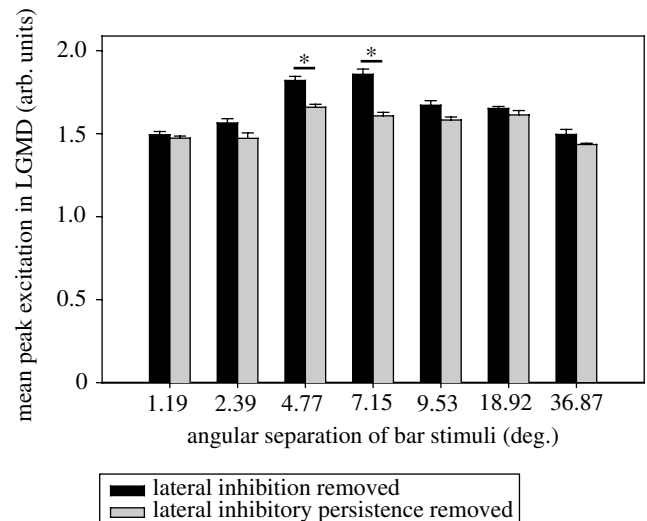


Figure 10. Mean peak LGMD excitation ($n = 20$ – 25 trials per bar separation, mean $\pm$ SEM) in response to two bar stimuli with varying angular separations crossing the camera's field of view. For large and small bar separations, the removal of lateral inhibitory persistence had the same effect as the removal of lateral inhibitory connections entirely. However, for optimal bar separations of between 4.77 and 7.15° , the removal of lateral inhibitory persistence did not cause peak LGMD excitation to reach as high a level as it did when lateral inhibitory connections were removed entirely. A two-way ANOVA test showed a significant interaction between lateral inhibitory condition and bar separation (see text). A *post hoc* Tukey test showed the difference between the LGMD response with lateral inhibitory persistence removed and lateral inhibition entirely removed to be significant ($P < 0.05$) at bar separations of 4.77 and 7.15° (indicated in plot by *).

of 4.77° and 7.15° and no significant difference at bar separations outside of this range. Therefore, persistent lateral inhibition at the S-cell layer could suppress the model LGMD's response over a range of stimulus separations whilst direct lateral inhibition between active processing channels could only occur when stimuli were optimally separated (figure 10).

3.4. The response of the model LGMD in a simple test environment

In a final experiment we tested the LGMD model's performance in a simple test environment (figure 11*a*). In these trials the robot first translated, with a whole-field sinusoidal grating displayed to its left (figure 11*a*(i)). It then rotated with the same grating displayed to its front and left side (figure 11*a*(ii)) before approaching a spherical stimulus on a direct collision course with no grating displayed (figure 11*a* (iii)). In these trials the model LGMD was not used to control the robot in order that visual stimuli were the same for both model conditions, but the experimental environment allowed the LGMD's performance during a simple task to be assessed. The intact LGMD model (figure 11*b*) produced two spikes at the onset of movement but then did not respond during the first (whole-field image

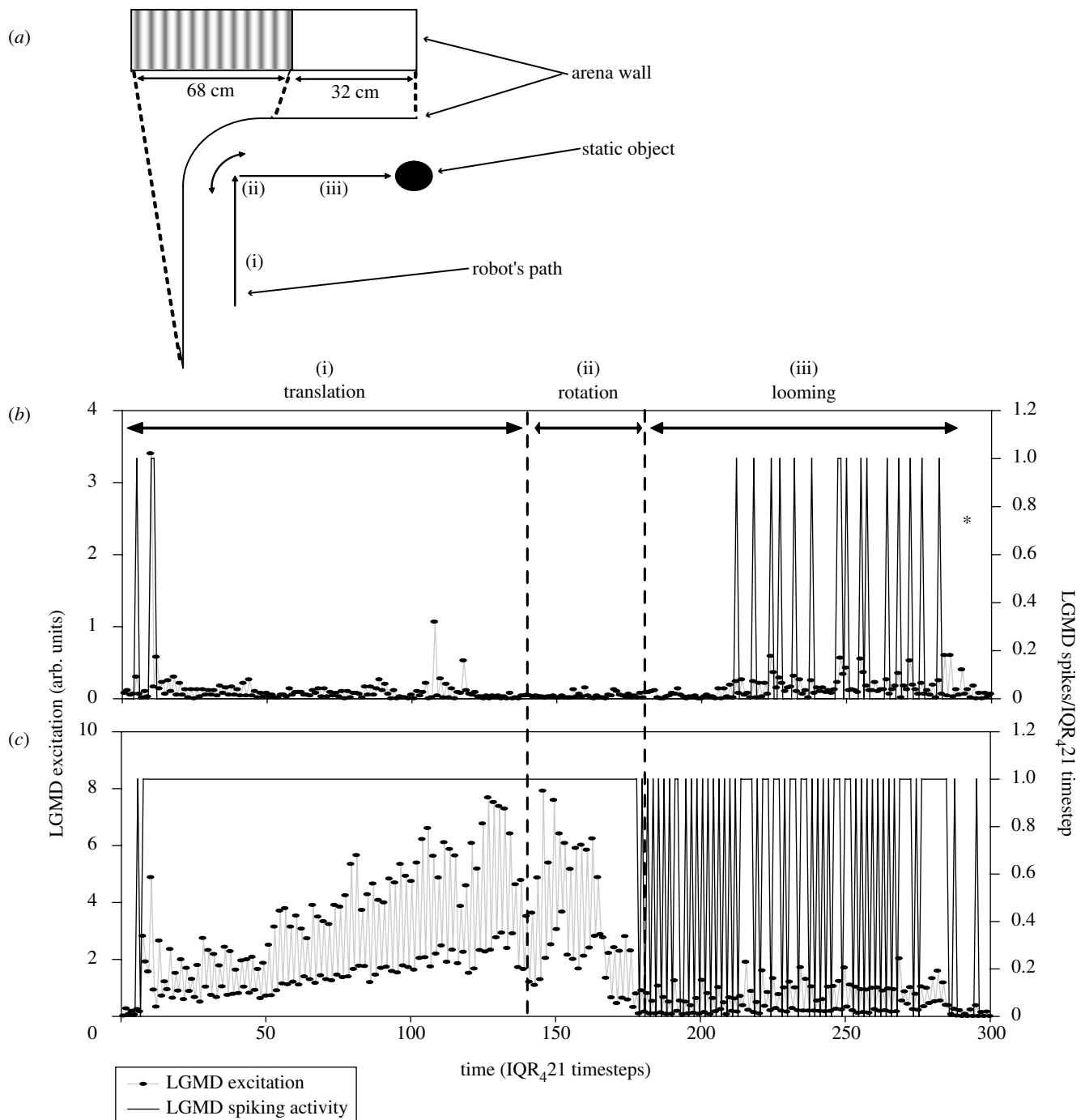


Figure 11. The response of the model LGMD in a simple test scenario. (a) The robot's task was to detect collision, but not rotation, in a simple structured environment. The robot first moved 27 cm at a speed of 19 mm per timestep with a sinewave grating presented to its left (i). It then made a 90° turn at 2.4° per timestep with the same grating displayed to its left (ii). Following this turn, the robot moved a further 27 cm at 19 mm per timestep towards an 80 mm diameter black sphere presented on a collision course. During this phase of the robot's approach a white arena wall replaced the sinewave (iii). (b) The complete LGMD model responded briefly to the start of movement but not to the first stage of approach (i). It produced no spikes during rotation (ii), but responded strongly during the final stage of approach towards the colliding object (iii). The burst of spikes in response to this object are terminated as the object leaves the camera's field of view by feed-forward inhibition (*). (c) With lateral and feed-forward inhibition removed, the model responded strongly to translation in front of the sinewave grating and rotation ((i) and (ii)). Separate excitation events can be seen in (i) and (ii) as a result of excitation fading as the robot stops before turning or translating. The model LGMD also responded to potential collision (iii) but with less spikes than were elicited by whole-field movement. Spikes in response to the loom were not terminated at the end of approach by feed-forward inhibition and the model LGMD's response to rotation and looming are not easily distinguished. In all cases the robot maintained a distance of 70 mm from the sinewave grating which had a stripe period of approximately 8° at the camera. Note that the LGMD excitation axes in (b) and (c) have different scales.

movement) phases of the robot's task. It then responded with a strong burst of spikes to the colliding stimulus. In this condition the LGMD's spikes warned of collision but were suppressed during whole-field movements. With lateral and feed-forward inhibition removed (figure 11c), the model LGMD was strongly excited by both translation and rotation, spiking constantly through these phases of approach. Its spike rate declined slightly during approach to the colliding object but a distinct burst of spikes in response to the object was not discernable due to residual excitation from the previous whole-field movements. Therefore, with no inhibition the model could not effectively discern between looming and whole-field stimuli.

4. DISCUSSION

The responses of the locust LGMD and DCMD neurons to whole-field visual stimuli are effected by retinally- and centrally-generated saccadic suppression (Rowell *et al.* 1977; Zaretsky & Rowell 1979; Zaretsky 1982). The retinal component of this suppression was hypothesized to result from the differential activity of lateral and feed-forward inhibitory pathways in the LGMD's input architecture (O'Shea & Rowell 1975; Rowell *et al.* 1977). We have confirmed these differential roles using a computational model of the LGMD's input architecture linked to a mobile robot (Rind & Bramwell 1996; Blanchard *et al.* 2000). This model is able to ignore saccadic stimuli and detect potential collision in a simple test scenario.

4.1. A mechanism of retinally-generated saccadic suppression

The complete LGMD model responded briefly to the initial movement of a whole-field visual stimulus but was suppressed as image motion continued in the same way that the locust LGMD responds to such a stimulus (Rowell *et al.* 1977). In the absence of lateral inhibition, the model LGMD responded strongly throughout the presentation of a whole-field stimulus due to increased excitation reaching it from its afferents. In the absence of feed-forward inhibition, the model LGMD received a similar excitation profile to the intact network but produced an increased burst of spikes at the onset of saccadic movement. In the locust LGMD, high contrast frequency gratings elicit feed-forward IPSPs in the LGMD which remove these spikes from its response (Rowell *et al.* 1977). Thus, feed-forward inhibition suppresses a model LGMD response to rapid, acceleratory image movements as robot rotation begins, and lateral inhibition suppresses the model LGMD response to sustained image movements as the robot reaches its constant rotation speed. Together these mechanisms provide a complete system of retinally-generated saccadic suppression. It is worth noting that even the low contrast frequency gratings used in our study elicited feed-forward inhibition in the model LGMD, unlike the real LGMD where these are only elicited at higher contrast frequencies (Rowell *et al.* 1977).

Because the locust LGMD responds to looming objects and may mediate escape from a looming predator (O'Shea *et al.* 1974; Rind & Simmons 1992; Robertson & Reye 1992; Robertson & Johnson 1993; Gray *et al.* 2001; Rind & Santer 2004), it is crucial that this neuron is not excited as the locust produces a voluntary saccadic head movement (Kien & Land 1978) in order to avoid false collision alarms. Retinally- and centrally-generated mechanisms work together in the locust LGMD pathway to mediate saccadic suppression (Zaretsky & Rowell 1979; Zaretsky 1982). Although retinally-generated suppression is weaker than that mediated centrally (Zaretsky 1982), it may still play an important role. In locusts, unintentional flight deviations would not be accompanied by a corollary discharge. Therefore, a retinally-generated component of saccadic suppression may be crucial in suppressing an avoidance behaviour in this inappropriate behavioural context. It is also important to note that some large-field optomotor neurons of insects, such as the horizontal system and vertical system neurons of the fly (Hausen 1976; Egelhaaf *et al.* 1989; Krapp & Hengstenberg 1996), respond particularly to optic flow patterns resulting from self-movement and may be involved in their correction. These must, therefore, not be saccadically suppressed like the locust LGMD neuron and may lack lateral and feed-forward inhibitory connections like those of the LGMD.

4.2. Lateral inhibitory action

We found that the model LGMD response to a single traversing bar was suppressed by lateral and feed-forward inhibition and that this effect was due to lateral inhibition spreading in advance of the moving bar and persisting in areas of retina which were soon to be stimulated as the bar advanced. When stimulated by two moving bars, the response of the LGMD was suppressed via two mechanisms—persistent lateral inhibition at the S-cells accounted for the suppression of the LGMD response when bars were separated by a very large or small amount, whilst direct lateral inhibition, triggered by one bar and directly acting on the processing channels excited by the second, contributed by a small amount to the suppression of the model LGMD at optimal bar separations.

In the locust, these direct lateral inhibitory effects could operate over a wider range of stimulus separations if the delay at these connections were subject to motion adaptation, as has been suggested to operate in fly elementary motion detectors (e.g. Maddess & Laughlin 1985; Clifford & Langley 1996). A more pertinent result is that the persistence of lateral inhibition is crucial to the operation of retinally-generated saccadic suppression by lateral inhibition. Persisting lateral inhibitory effects may allow retinally-generated saccadic suppression when a locust saccades or turns in its visually sparse natural environment of desert or savannah areas (Uvarov 1977). Furthermore, the persistence of lateral inhibition in rabbit directionally-selective (DS) ganglion cells results in an increased suppressive effect between two bar stimuli at increased visual stimulus velocities (Stasheef & Masland 2001). As the majority of lateral

inhibitory effect in the LGMD model resulted from its persistence, if this persistence were reduced, the model should then show saccadic suppression only at faster image velocities. Additional experimentation is required to investigate whether the persistence of lateral inhibition is also crucial to the tuning of saccadic suppression to image velocity in the locust LGMD neuron.

4.3. Saccadic suppression in vertebrates

Lateral inhibitory interactions are also present in vertebrate eyes (e.g. Balboa & Grzywacz 2000), so might the mechanism of retinally-generated saccadic suppression we find in the model LGMD operate in vertebrates?

In the vertebrate visual system, saccadic suppression acts on movement-detecting pathways during rapid saccadic eye movements and not during slow tracking eye movements. Thus any mechanism of saccadic suppression should also only be effective for rapid real or simulated saccades in these species. In the locust, lateral inhibition is activated selectively by slow-moving grating stimuli (e.g. Gabbiani *et al.* 2002) and therefore does not match the properties of saccadic suppression in vertebrates. This may result from the differing metrics of saccades in locusts and vertebrates and the vulnerability of locusts to relatively slow flight course deviations.

Nevertheless, a component of saccadic suppression by lateral inhibition could operate in vertebrate eyes, although to do so lateral inhibition would need to act selectively at higher image velocities. DS ganglion cells in the rabbit retina experience lateral inhibition (Stasheef & Masland 2001). This inhibitory effect is dependent upon the speed that two bar stimuli traverse the eye—for a given inter-bar separation the DS ganglion cell's response to the second bar is always greater at slower speeds due to inhibition fading more during the longer time interval between the stimuli (Stasheef & Masland 2001). Although rabbits perform saccadic eye movements (Collewijn 1977), the ganglion cells have not been shown to play a role in saccadic suppression. Nevertheless, these data indicate that lateral inhibitory connections exist in the rabbit eye that are able to have their effect only at higher stimulus speeds, a mechanism that may help lateral inhibition-mediated retinal saccadic suppression to operate in vertebrate eyes and explain the effectiveness of this suppression only at high saccadic velocities. The DS ganglion cells also demonstrate the presence of lateral inhibition in motion-detecting visual pathways in vertebrate eyes.

Furthermore, the threshold for the detection of a test stimulus during a saccade by human subjects can be altered by the background over which the eye saccades (Mitrani *et al.* 1975). This detection threshold is higher when numerous boundaries cross the eye's field of view and it is thought to be elevated by long range lateral inhibitory connections effective over around 1° , present in the peripheral retina and excited as a result of moving edges in the background to the test stimulus (Mitrani *et al.* 1975). Therefore, lateral inhibition may be one mechanism of retinally-generated saccadic suppression common to the locust LGMD and also to movement detecting neurons in some higher organisms.

Although feed-forward inhibition is not widely known in vertebrate visual systems, some studies point to its involvement in saccadic suppression. A depression in the excitability of relay cells in the lateral geniculate nucleus of cats occurs in response to saccade-like image movements (Noda 1975). This suppression could not result from a central signal because the cat's eyes were not actively moving and thus may indicate inhibition feeding forward to these cells from the retina.

It is important to note that the mechanism of retinal saccadic suppression we report cannot account for all the properties of saccadic suppression observed in all species which, in many cases, must result from a central mechanism (e.g. Fischer *et al.* 1996). Nevertheless, the mechanism of saccadic suppression we report may still operate in addition to a central mechanism in at least some vertebrate species.

4.4. Saccadic suppression in robots

The presence of a retinal saccadic suppression mechanism in the LGMD model is an important property that should allow its continued development for real world collision detection applications (Blanchard *et al.* 2000). The complete LGMD model is able to ignore saccadic stimuli whilst still effectively detecting collisions. Its response to each of these stimuli could be easily distinguished. Without inhibitory connections, the LGMD model responded indiscriminately to whole-field and looming stimuli which would result in false collision alarms in real collision-detection applications. Our simple test stimuli represent a structured and simplified real-world environment and, under these conditions, retinally-generated saccadic suppression is sufficient to prevent a model LGMD response to whole-field stimuli. However, under more complex unstructured visual conditions, it remains to be seen whether a central inhibitory signal is also required to suppress an LGMD response to saccade-like stimuli.

Mobile robots are powerful tools for the development of such real-world visual sensors as they allow the sensors to be tested in complicated environments that are subject to shadow and lighting effects. These conditions are difficult to simulate computationally but, in order for a sensor to be effective in the real world, it must function in complex visual environments.

This work was supported by the Gatsby Charitable Foundation, BBSRC and EU (LOCUST IST-2002-38097). We thank Mark Blanchard for assistance with setting up the robotic and computational equipment used in this study, and Alex Thiele and Peter Simmons for critically reading the manuscript.

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