

Neural Network Based on the Input Organization of an Identified Neuron Signaling Impending Collision

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SUMMARY AND CONCLUSIONS

1. We describe a four-layered neural network (Fig. 1), based on the input organization of a collision signaling neuron in the visual system of the locust, the lobula giant movement detector (LGMD). The 250 photoreceptors ("P" units) in layer 1 are excited by any change in illumination, generated when an image edge passes over them. Layers 2 and 3 incorporate both excitatory and inhibitory interactions, and layer 4 consists of a single output element, equivalent to the locust LGMD.

2. The output element of the neural network, the "LGMD", responds directionally when challenged with approaching versus receding objects, preferring approaching objects (Figs. 2–4). The time course and shape of the "LGMD" response matches that of the LGMD (Fig. 4). Directionality is maintained with objects of various sizes and approach velocities. The network is tuned to direct approach (Fig. 5). The "LGMD" shows no directional selectivity for translatory motion at a constant velocity across the "eye", but its response increases with edge velocity (Figs. 6 and 9).

3. The critical image cues for a selective response to object approach by the "LGMD" are edges that change in extent or in velocity as they move (Fig. 7). Lateral inhibition is crucial to the selectivity of the "LGMD" and the selective response is abolished or else much reduced if lateral inhibition is taken out of the network (Fig. 7). We conclude that lateral inhibition in the neuronal network for the locust LGMD also underlies the experimentally observed critical image cues for its directional response.

4. Lateral inhibition shapes the velocity tuning of the network for objects moving in the *X* and *Y* directions without approaching the eye (see Fig. 1). As an edge moves over the eye at a constant velocity, a race occurs between the excitation that is caused by edge movement and which passes down the network and the inhibition that passes laterally. Excitation must win this race for units in layer 3 to reach threshold (Fig. 8). The faster the edge moves over the eye the more units in layer 3 reach threshold and pass excitation on to the "LGMD" (Fig. 9).

5. Lateral inhibition shapes the tuning of the network for objects moving in the *Z* direction, toward or away from the eye (see Fig. 1). As an object approaches the eye there is a buildup of excitation in the "LGMD" throughout the movement whereas the response to object recession is often brief, particularly for high velocities. During object motion, a critical race occurs between excitation passing down the network and inhibition directed laterally, excitation must win this race for the rapid buildup in excitation in the "LGMD" as seen in the final stages of object approach (Figs. 10–12). The buildup is eliminated if, during object approach, excitation cannot win this race (as happens when the spread of inhibition laterally takes <1 ms Fig. 13, *D* and *E*). Taking all lateral inhibition away increases the "LGMD" response to object approach, but overall directional selectivity is reduced as there is also a lot of residual network excitation following object recession (Fig. 13*B*).

6. Directional selectivity for rapidly approaching objects is further enhanced at the level of the "LGMD" by the timing of a feed-forward, inhibitory loop onto the "LGMD", activated when

a large number of receptor units are excited in a short time. The inhibitory loop is activated at the end of object approach, truncating the excitatory "LGMD" response after approach has ceased, but at the initiation of object recession (* Figs. 2, 3, and 13). Eliminating the feed-forward, inhibitory loop prolongs the "LGMD" response to both receding and approaching objects (Fig. 13*F*).

INTRODUCTION

As an object moves directly toward the head, both the size of the image on the eye and the disparity between the images on the two eyes increase. Binocular interactions, such as the use of binocular disparity, have only exceptionally been found to underlie range estimation by invertebrates, mainly because there is little overlap between the visual fields of the left and right eyes and the absolute distances separating the two eyes are small (for a review see Schwind 1989). For many animals, a rapidly expanding dark image is a powerful stimulus eliciting an avoidance or escape reaction (Gibson 1958; Holmqvist and Srinivasan 1991; Schiff et al. 1962; Wang and Frost 1992). In the locust, two identified neurons, the lobular giant movement detector (LGMD) (O'Shea and Williams 1974) and the postsynaptic descending contralateral movement detector (DCMD) (Rind 1984; Rowell 1971), respond selectively to the images of an object approaching toward, as opposed to receding from, their eye (Rind and Simmons 1992). The DCMD can discriminate between approaching and receding objects using cues derived from one eye. The strongest response is given to an object approaching on a collision course with the eye, when collision is imminent. The critical image cues for the selective response to approaching objects have been isolated as an increase in the velocity of motion of the boundary edges of the image and a rapid increase in the amount of edge in the image (Simmons and Rind 1992). The critical image cues are extracted locally without reference to global image patterns. The use of more than one cue adds robustness to the DCMD response, enabling the neuron to respond reliably and quickly to an approaching object. When an object is on a collision course with the locust, both these cues will be maximized.

The receptive field organization of the LGMD and DCMD neurons had been explored extensively before their selective response to rapidly approaching objects was appreciated. The LGMD is the sole source of compound eye input to the DCMD, and spikes in the DCMD follow those in the LGMD one for one (Rind 1984). In the optic lobe, the LGMD receives excitatory input from a retinotopic array of small-field neurons, each excited transiently by changes in illumination (O'Shea and Rowell 1976). The excitatory inputs to

the LGMD occur over the dendritic fan of the neuron in the distal lobula. Lateral inhibition, which is a prominent feature of the input organization of the LGMD, occurs between the retinotopic afferent neurons responding to edge transitions of either the same (Edwards 1982; Rowell et al. 1977), or the opposite contrast polarity (Simmons and Rind 1992). This lateral inhibition occurs before the convergence of the retinotopic input onto the LGMD, and thus before the decrement-prone synapse between the afferents and the LGMD (O'Shea and Rowell 1975, 1976). Direct inhibition of the LGMD occurs in a region of the neuron proximal to the convergence of the excitatory afferents on the dendritic fan and is mediated by two classes of neuron excited either by light-dark or dark-light transitions (Rowell et al. 1977). These two classes of neuron constitute a feed-forward loop bypassing one or more tiers of processing distal to the LGMD (Rowell et al. 1977). The input organization of the LGMD and DCMD neurons are known to the extent that it should be possible to incorporate these features into a computational model. Edwards (1982) incorporated details of the input organization of the cockroach DCMD into a model to examine the effect of lateral inhibition on the response to a small spot of light whose intensity could be set experimentally. The model was used as an initial framework for developing the present network. For this network to be an adequate representation of the input organization of the LGMD neuron, its output must share the response properties of this neuron as described by Rind and Simmons (1992); in particular, it should show a selective response to approaching versus receding objects. This selectivity should be maintained over a range of approach speeds, object sizes, approach distances, trajectories, and contrasts (light vs. dark objects). The network should show a nondirectional response to objects that move with a constant velocity at a fixed distance from the eye and it should respond best to large objects moving rapidly. The network should share the same critical image cues for a selective response to object approach: directional responses should be produced to edges that change in either extent or velocity as they move. If the model performs in the same way as the LGMD neuron, it then will be possible to examine the mechanisms within the network that underlie the directional selectivity for objects moving in depth and, by analogy, to explore the possible mechanisms in the circuits that feed the LGMD neuron. For example, it will be possible to determine how the properties of the LGMD input organization generate the critical image cues for a selective response to an object approaching on a collision course (Simmons and Rind 1992).

In this paper, we describe a neural network that meets the above criteria and, therefore, could be considered an adequate representation of the input organization of the LGMD neuron. The network is quite simple and demonstrates the importance of the relative timing between excitation and inhibition for the selective response to approaching objects. A critical race between excitation passing down the network and inhibition directed laterally is essential to the rapid buildup of excitation in response to approaching objects. A feed-forward inhibitory loop, activated only when a large number of "photoreceptors" are excited, also contributes to directional selectivity. The feed-forward loop is strongly activated and truncates the excitatory "LGMD" response at

the end of object approach but at the beginning of object recession.

METHODS

The computer program is written and runs on a Research Machine PC with a 486, 33MHz processor, using software written in Borland Turbo C. Both the image and the neural network are realized in software. Input to the neural network is provided when a simulated object moves in three-dimensional space, creating image motion over the "eye" of the network (Fig. 1). The network incorporates the general features of a locust eye, including the input organization of the LGMD and DCMD neurons described above. The photoreceptors ("P" units) are excited by changes in levels of illumination, generated when an image edge passes over them. Excitation passes retinotopically down the network through layers 1–3 and is summed by the output unit in layer 4: the "LGMD". Inhibition passes forward and laterally or loops forward arriving after the convergence of the retinotopic projection onto the LGMD. Both inhibitory inputs are delayed, by 2–5 ms relative to the excitation passing down the network.

Network and its inputs

The inputs to the network are a series of computer-generated images of a moving object, one per millisecond of simulated time. The size of the object, its initial and final position in three-dimensional space, and its velocity are controlled for each simulation (Table 1). In layer 1, each image is mapped onto the array of photoreceptors, each of which views a narrow region of space separated from that of its neighbors by a minimum of 3.3 deg (Fig. 1 and Table 2). This angle is outside the locust range of 1.2–2.3 deg (Horridge 1978), but was chosen to spread the combined field of view of all 250 photoreceptors in space. Each facet is treated as having just one photoreceptor, a simplification which is justified functionally because all seven receptors making up the rhabdome in the locust eye look at the same region in space (Nilsson 1989). The angle between neighboring photoreceptors and the size of their receptive field increases progressively toward the edges of the array, mimicking the curvature of the locust eye. Each photoreceptor (layer 1, P unit) in the model responds with a brief (1 ms) excitation to a change in level of illumination (Fig. 1). The layer 1, P unit is thus a composite between a photoreceptor and one or more postsynaptic neurons in which responses to light on and off are processed to give the same signals (O'Shea and Rowell 1976). The excitation in the P unit is extremely transient and marks the passage of an edge with great precision. Similar response time courses with a tight coupling of response and stimulus timing have been observed in "transient cells" in the locust medulla responding to small light increments or decrements (O'Carroll et al. 1992; Osorio 1987, 1991).

The excitation from the P units is passed on to two units in layer 2: an excitatory "E" unit, and an inhibitory "I" unit. Excitation and inhibition from the layer 2 units are summed by "S" units in layer 3, which excite the "LGMD" in layer 4. Synaptic and conduction delays within and between layers can be set independently. However, for the simulations described here, delays at excitatory connections between layers are set to 0 ms, whereas delays on inhibitory connections vary between 1–4 ms. Excitation of a layer 2 E unit follows activation of the P unit feeding it, unless the unit is within its refractory period. In layer 2, each E unit passes excitation to one layer 3 S unit in the same retinotopic position and each I unit passes inhibition laterally to two rings of S units, centered on the I unit. The 6 nearest and 12 next-nearest neighbors of each I unit are specified using look-up tables. The inhibition passed from the I unit to each nearest and next-nearest S unit is always divided by the number of such connections made by the I unit, thus 1/6 of the input excitation is passed to each nearest and 1/

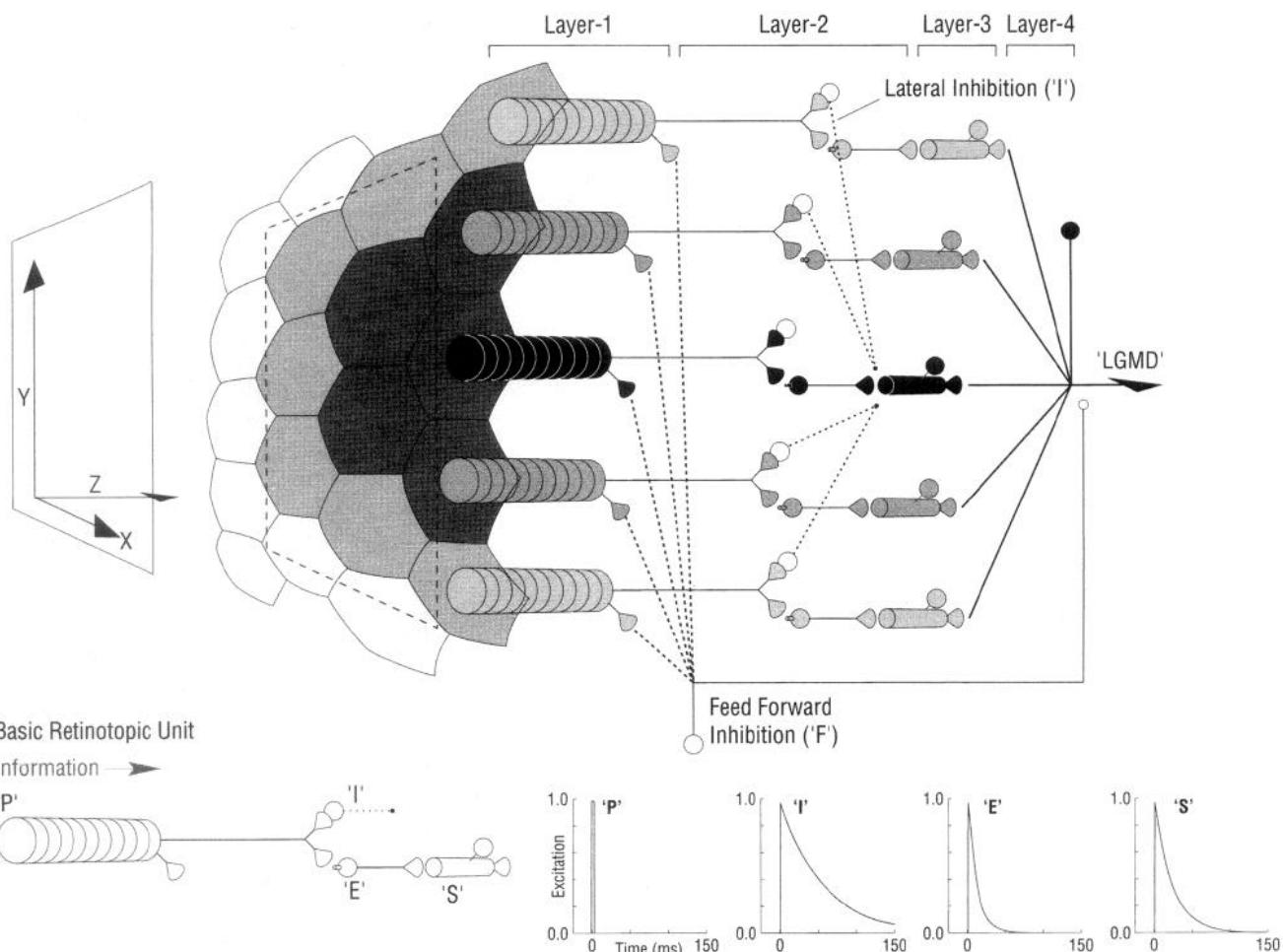


FIG. 1. Schematic representation of neural network. Inputs to network were a series of computer-generated images of a moving object. Input organization of the basic retinotopic unit of the network is labeled. Output activity of 250 of these units converge on the "lobula giant movement detector" ("LGMD") unit. In layer 1, images were mapped onto the hexagonally packed photoreceptors, each of which viewed a narrow region of space, separated from that of its neighbors by 3.3 deg. Each photoreceptor (P unit, layer 1) in the model responded with a brief (1 ms) excitation to a change in level of illumination. In layer 2, this excitation was passed to 3 units: E, I, and F. When excited, E passed excitation to a layer 3, S unit in the same retinotopic position; I passed inhibition laterally to the 6 nearest and 12 next-nearest layer 3 S units and F fed inhibition forward bypassing layer 3. F was only active when a large number of photoreceptors were activated in a short time. E and I inputs were summed linearly by each S unit in layer 3 until a threshold level of excitation was reached and a spike was produced. A refractory period followed such activation, during which the neuron could not be activated, and excitation decayed exponentially. Layer 4 of the model consisted of a single "LGMD" unit, which summed excitation from all active S units and inhibition from the F unit. In each layer, proximity to the central retinotopic unit is indicated by the shade of grey. Time course of activation of each different unit is shown at bottom. P, photoreceptive unit (layer 1); I, laterally projecting, inhibitory unit (layer 2); E, excitatory unit (layer 2); F, feed-forward inhibitory unit; S, excitatory summing unit (layer 3); and "LGMD", final output unit (layer 4).

12 to each next-nearest S unit. This inhibition passed on by an I unit to each nearest and next-nearest S unit then can be altered further by changing the synaptic weighting of the I unit input. This synaptic weighting is expressed as the percent of I unit activation

TABLE 1. Stimulus for simulated edge translation and object approach

Stimulus	Edge Translation	Object Approach
Initial position x, y, z , mm	-99, 0, 50	0, 0, 400
Dimensions $l \times h$, mm	100 × 80	75 × 75
Plane of motion, (x, y , or z)	x	z
Direction and distance, mm	70	-400
Velocity, m/s	0.75	10

Neural network responding selectively to approaching objects.

TABLE 2. Parameters for neural network

P-unit	Network				
	Delay, ms	Inter P Spacing, o	Distance to Screen, mm		
0	3.3	100			
	T _{const} , ms	T _{refr} , ms	I _{Thres} , 0–1	Delay, ms	Weight, %
E-unit	12.33	0	0	0	100
I-unit n	55.00	0	0	2	170
$n + 1$				4	70
S-unit	22.20	2	0.1	0	100
F-unit	*	0	0.05	4.5	*

* Depends on the rate of change in total P activity. T_{const}, time constant; T_{refr}, refractory time; I_{Thresh}, threshold activation.

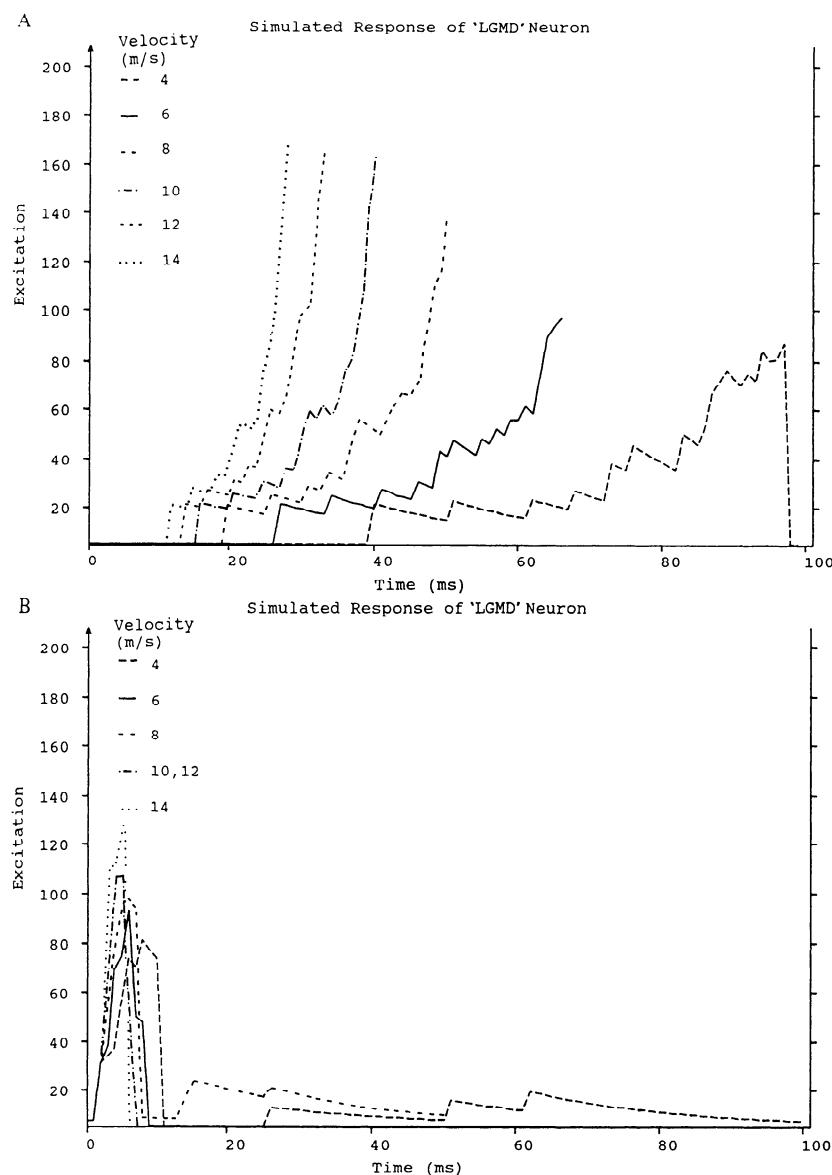


FIG. 2. Response of "LGMD" to object motion. *A*: object approach on a collision trajectory. *B*: object recession along the same path. Velocities of 4–14 m/s were simulated. Other stimulus details and network parameters were as in Table 1. Activity in the "LGMD" was plotted at 1-ms intervals throughout each simulation.

passed across to each S unit and is $(I \text{ unit activity}/6) \times \text{percent}$ for nearest S units and $(I \text{ unit activity}/12) \times \text{percent}$ for next-nearest S units. Unless specifically mentioned, these weightings are 170% to the nearest and 70% to the next-nearest S units. The I unit inhibition to the nearest, and to the next-nearest layer 3 S units also is delayed by a selected amount, relative to the excitatory input. This results in a balance between excitation passing from layer to layer down the network and inhibition directed laterally. The maximum possible inhibition onto an S unit when all surrounding I units are active, expressed as a percent the initial P unit activation entering the pathway, is $(6 \times 1/6 \times 170\%)$ from the nearest neighbor I units plus $(12 \times 1/12 \times 70\%)$ from the next-nearest neighbor I units = 240%. However, for the 2 or 4 ms conduction delays to the nearest, and to the next-nearest S units, the time constant for the I unit results in only a proportion of this activation $(170\% \times 0.96)$ plus $(70\% \times 0.93) = 228\%$ being passed to S units. The lateral inhibition exhibited by the LGMD network has been shown to be stimulus rather than response dependent, which means that the system remains stable even when the total inhibition generated by the network is greater than the response that produced it (Edwards 1982; O'Shea and Rowell 1975). This means that it is not essential to the stability of the network for the

total inhibition, induced by each I unit, to balance the excitation received by the I unit initially.

The E and I inputs are summed linearly by each S unit in layer 3 until a given threshold level of excitation is reached and a "spike" is produced (Fig. 1). After the peak of a spike, voltage declines exponentially with time and is followed by a refractory period. This phase of the S unit response is independent of any inhibitory input. Buildup of excitation in an S unit is not shown, only its suprathreshold output. Layer 4 of the model consists of a single "LGMD" unit, which linearly sums excitation from all active S units and inhibition, delayed by 2–5 ms, from the inhibitory F unit. This sum is expressed as a voltage, rather than a spiking output because the input-output function of the LGMD neuron is not known. The F unit in the network constitutes a feed-forward pathway, by-passing layer 3, and is only active when a set number of P units (~ 50) are activated in a short time. For each simulation, the threshold number of photoreceptors excited before activation of the loop occurs and the activity in the feed-forward inhibitory F unit can be set. The initial increase in activity and then the rate of decay both are controlled by the rate of P unit activation or inactivation.

After activation, of an E, I, or S unit excitation in it declines exponentially (Fig. 1). This form of activation is of a similar form

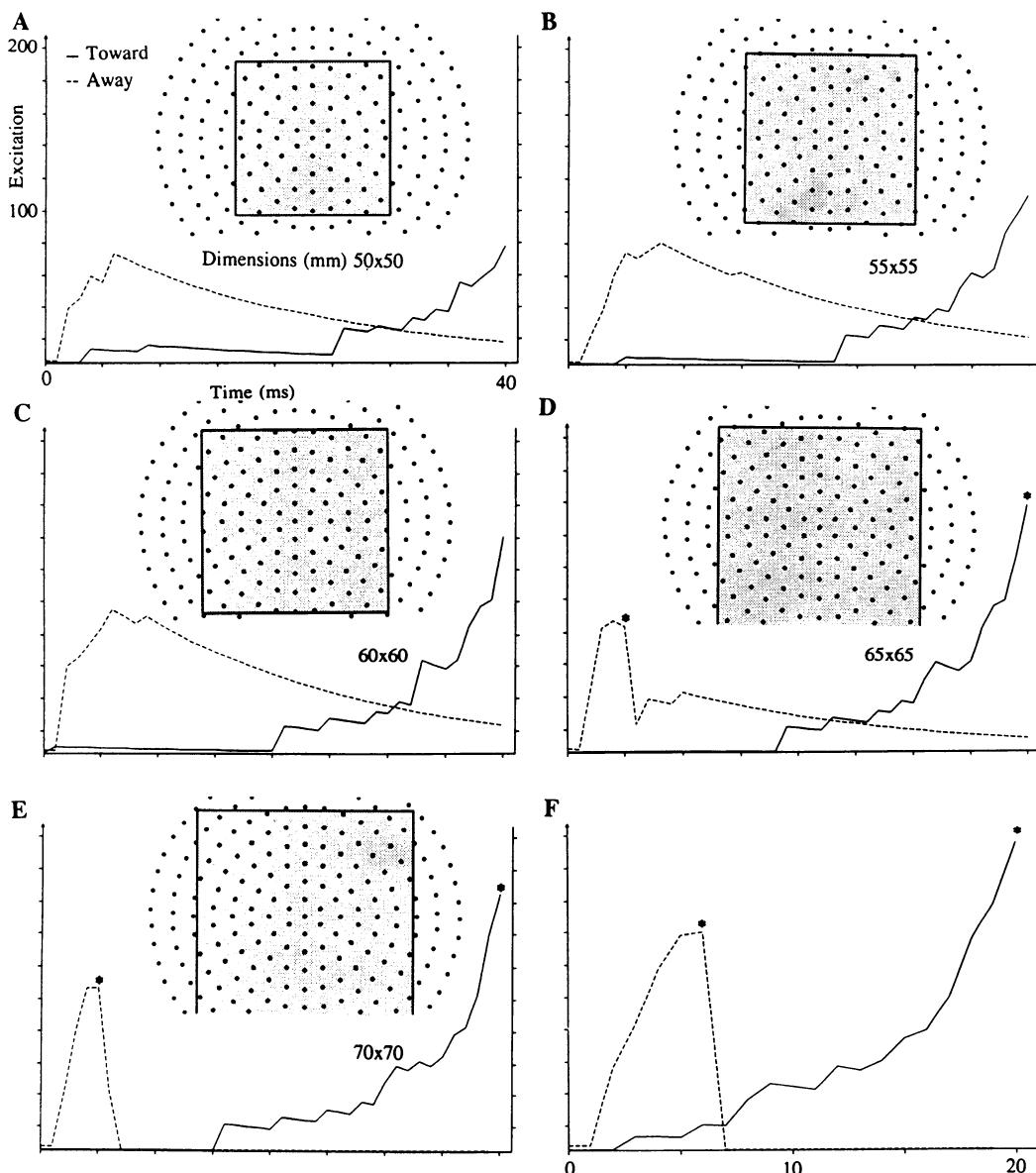


FIG. 3. Effects of object size (*A–E*) and starting distance (*F*) on directional selectivity. Response of "LGMD" is plotted to objects ranging in size from 50–70 mm and approaching on (—), or receding from (---), a collision course with eye. Object size in millimeters, all objects were square: *A*, 50; *B*, 55; *C*, 60; *D*, 65; *E* and *F*, 70. In *F*, object was closer to the eye: it approached from, and receded to, 300 mm from "eye". Other stimulus conditions and network parameters were as in Table 1. Activity in the "LGMD" was plotted at 1-ms intervals throughout simulation. *, onset of feed-forward loop inhibition onto "LGMD". Insets show image of object mapped onto input array, at object's closest distance to eye.

to that used by Werblin (1991) to model activity in the tiger salamander retina. Time constants are all set within physiological limits. The time constant for the I unit is the longest at 55 ms, a value consistent with γ -aminobutyric acid-B (GABA_B)-mediated inhibition (Werblin 1991). Unless otherwise stated, in each simulation the network is allowed to adapt to the presence of the object on the eye before motion begins. This process of adaptation is defined relative to the declining activity of E units in layer 2. All values chosen for the parameters of the network fall within experimentally observed limits for the locust nervous system. The output of the network is resistant to small alterations in these parameters.

Monitoring network activity during each simulation

During each simulation, a graphical display is available at the end of each simulated ms for the image on the array of P units in

layer 1; activity in each I unit in layer 2; and activity in each S unit in layer 3. The retinotopic position of each unit is preserved in the display, with the level of excitation indicated by a circle whose radius is proportional to excitation level. Activity in the "LGMD", the output element in layer 4 of the network, is displayed at the end of each simulation as a graph of excitation, on a scale of 0–400, against time. Taken together, these outputs allow activity in a particular element in any layer to be related to both the object attributes that produce it, and the phase of the final output response to which it contributed. Tables 1 and 2 give the parameters used for both stimulus and network to produce the results shown in the initial figures in this paper. Object motion occurs relative to a screen 100 mm from the P units of the eye. The distance and position of the object relative to the screen is given by three values: *X*, corresponding to horizontal position; *Y*, corresponding to vertical position; and *Z* corresponding to distance (see Fig. 1). Object dimensions, object velocity, the direction and length of path are speci-

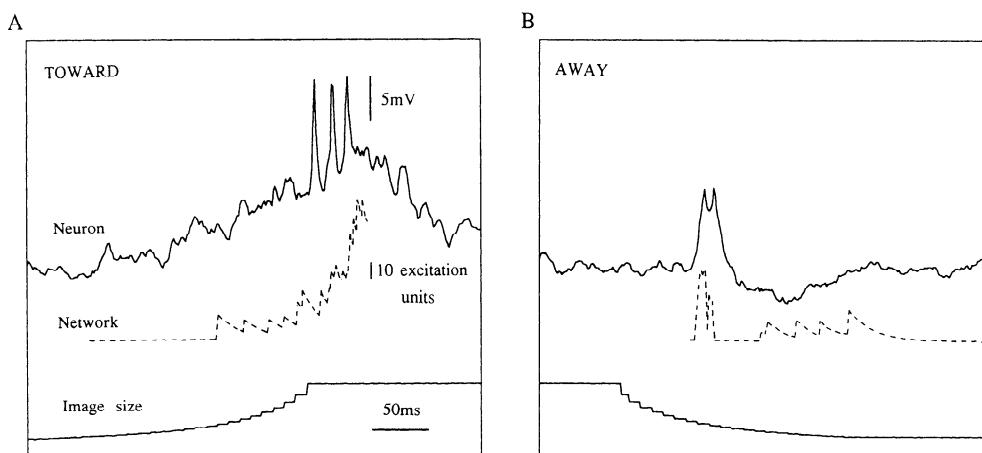


FIG. 4. Response of the network "LGMD" and the locust LGMD compared. *A*: object approach on a collision trajectory. *B*: object recession along same path. Movements of a 75-mm object occurred at a velocity of 2 m/s over a 500 mm distance, from 600 mm to within 100 mm of the eye. In each panel, *top* trace (—) shows response of LGMD recorded from its dendrites in optic lobe; *middle* trace shows output of network "LGMD" and *bottom* trace monitors image size of approaching or receding object. An upward deflection indicates an increase in image size. Image size ranged between 7.2–41 deg at eye. Beginning of network response was aligned with first observable response in LGMD neuron. This was necessary as network was set up without a delay in photoreceptor unit response after stimulus movement (see P unit, Table 2).

fied, in millimeters or meters per second. Motion in the Z direction toward or away from the P units always occurs with at a constant velocity. When a particular set of network parameters are specified and the simulation performed repeatedly, the network activity and "LGMD" output are identical on each occasion.

RESULTS

The results are divided into three parts. The first section seeks to establish that the network behaves like the locust LGMD neuron. The second section looks at processes in the network underlying this behavior and the final section assesses the importance of these processes by altering each one separately and looking at the response of the network. The response of the network is always the same to a repeated stimulus.

"LGMD" response to object approach versus recession

In the following experiments, the network "LGMD" is challenged by the kinds of stimuli that were used to establish the locust LGMD/DCMD neurons as collision detectors and to examine the critical image cues for this discrimination. (Rind and Simmons 1992; Simmons and Rind 1992). Objects either move in depth relative to the eye or laterally at a fixed distance from the eye. The activity in the "LGMD" in layer 4 of the network is recorded at millisecond intervals throughout each simulated movement (Table 1 for details of the two stimulus configurations). Directionality of the "LGMD" response to opposing directions of movement is assessed by comparing either the peak amplitude of its response or the duration of the rising phase of its response. These measures were adopted because spike production by the locust LGMD has been found to require a rising, or maintained membrane potential (Rind 1996).

When the network is challenged with objects approaching or receding, at all velocities tested, the "LGMD" responds directionally, preferring object approach to recession (Fig. 2). The directionality of response is the same for both light and dark objects—eliminating

luminance change as a cue for the directionality. Excitation in the "LGMD" increases throughout the approach of an object. The faster the approach, the greater the rate of increase in excitation and also the greater the final level of excitation, reaching a maximum level at approach velocities of 10 m/s (Fig. 2). This closely parallels the response of the locust LGMD as described in Fig. 6, Rind and Simmons (1992). The response latency, measured as the first "LGMD" excitation, decreases with increases in approach velocity. The "LGMD" responds throughout object approach and its response is only brought to an end after object motion has ceased. This contrasts markedly with the "LGMD" response to receding objects; this response occurs as a brief peak, with a rising phase of only 4.5–8 ms, soon after the start of object movement. Like the locust LGMD (Fig. 6, Rind and Simmons 1992), the "LGMD" response amplitude increases as velocity increases but response latency remains constant. At the slowest velocities of object recession, there are a series of small peaks in LGMD excitation that follow the initial peak.

Directional "LGMD" responses also are found for a wide range of object sizes and distances from the eye (Fig. 3, A–F). The excitatory response to approaching objects is of greatest amplitude to the largest objects simulated as is observed for the locust LGMD (Fig. 7D, Rind and Simmons 1992). In every simulation, the rising phase of the "LGMD" response is longer in response to object approach than it is to object recession. "LGMD" directionality increases with increasing object size, reaching a maximum with an object of 70 × 70 mm (Fig. 3E). With objects of this size, the "LGMD" response to object recession is very brief, lasting only 5 ms, with a rising phase of 2–3 ms. Objects ≤65 × 65 mm produce progressively less excitation in the "LGMD" during object approach, but with the smallest objects, the response becomes prolonged after motion has ceased. In contrast, the response during object recession grows more prolonged as the size of object decreases. These two effects decrease the directionality of the "LGMD" to smaller-sized objects. Beginning the approach from closer to

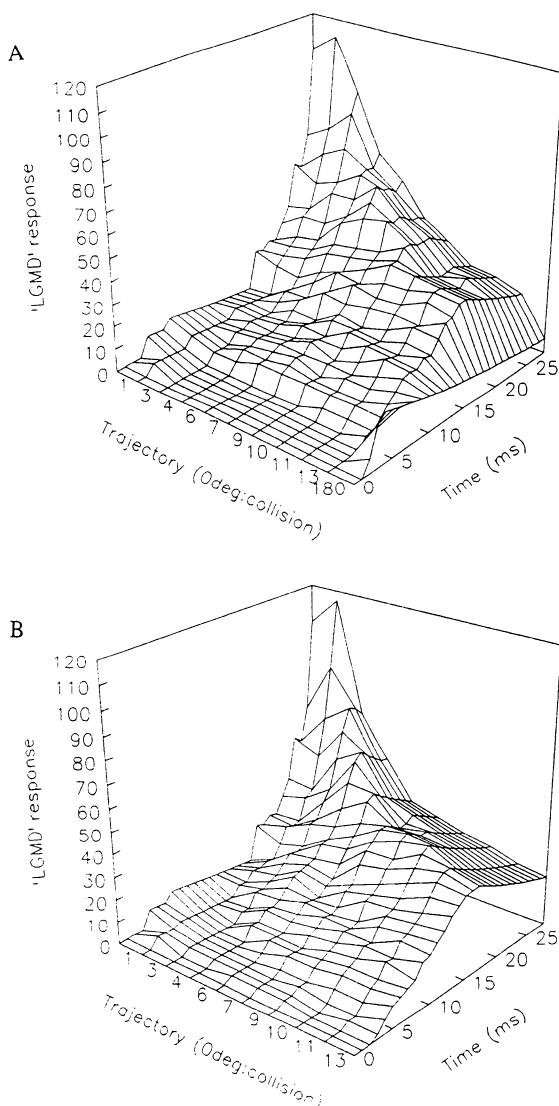


FIG. 5. Collision vs. noncollision trajectories. Response of the “LGMD” to a square object 50 mm in size, approaching eye at 15 m/s. Approach trajectories were successively displaced: *A*, in the *X* direction; *B*, in the *X* and *Y* directions, away from a collision path (for *X* and *Y* directions, see Fig. 1). Other stimulus details and network parameters were as in Table 1. Activity in “LGMD” was plotted at 1-ms intervals throughout each simulation. Greatest response was given in response to a simulated trajectory 1.4 deg from a direct collision course.

the eye does not change the overall form or directionality of the “LGMD” response (Fig. 3*F*, note expansion of *x* axis).

When the responses of the network “LGMD” and the locust LGMD (recorded as in Rind 1996) are compared with stimuli of the same size, moving at the same velocity, from the same distance and on the same trajectory (Fig. 4, *A* and *B*), the shape and timing of the two responses are very similar. The response of the network to a distant approaching object begins after that of the neuron as there is a longer interval before any of the image edges pass over an input unit of the network compared with the eye. This difference can be accounted for by the 20-fold decrease in number of input elements in the network (250) compared with the locust eye (5,000).

The excitatory response of the “LGMD” is greatest for objects approaching on a collision course. Figure 5 shows

excitation in the “LGMD” plotted as a function of trajectory. In all these simulations an object 50 × 50 mm in size approaches the eye at a velocity of 15 m/s. These particular attributes are chosen to maximize both the time the object stays within the receptive field of the eye and the excitation evoked by the object. In a series of 10 approaches, the object is made to deviate by successive increments of 1.43 deg from a collision trajectory (other stimulus details as in Table 1). Deviations occur either in the horizontal plane alone (Fig. 5*A*) or in a plane midway between the horizontal and vertical (Fig. 5*B*). The greatest “LGMD” response is given to objects approaching within 3 deg of a direct collision course with a peak in response with a slight (1.4 deg) deviation from a direct collision course (Fig. 5, *A* and *B*). As the object was 5 × 5 mm in size, trajectories within 3 deg of a direct approach will still result in collision between object and eye.

“LGMD” directional selectivity to horizontal motion in the *X-Y* plane

The network does not respond directionally to constant velocity motion in the *X-Y* plane (parameters in Table 1). The leading edge of a bar is made to move laterally at 0.75 m/s, corresponding to an angular velocity over the “eye” of 287 deg/s, a velocity of motion similar to that used in a study of the response of the LGMD neuron (Fig. 5, Simmons and Rind 1992). The overall form and amplitude of the “LGMD” response to rightward (solid line Fig. 6) versus leftward (dashed line Fig. 6) edge movement is very similar (the saw-toothed appearance of each the curve is due to successive stimulation of aligned P unit receptive fields in the input array). From these curves, it is seen that the network, like the LGMD, does not respond preferentially to one particular direction of motion in the *X-Y* plane. This result is confirmed for a range of edge velocities and extents. Similar responses are recorded for motion of a bar rather than a single edge. With constant velocities of edge movement, the “LGMD” response increases as edge velocity increases over the range tested: 380 deg/s (1 m/s) – 1,150 deg/s (2.75 m/s). The network responds most strongly to large objects moving at high velocities.

Processes shaping network responses to moving objects

In the second part of this paper, we examine the mechanisms underlying the response of the “LGMD” to moving objects. We will look into the network to see what happens in layers 1–3 during object motion and test the importance of specific features of the network, such as lateral inhibition and feed-forward inhibition, by altering each process in turn and examining its effect on the selective response of the network.

First we will examine the critical image cues for a directional response by the network “LGMD” and the importance of lateral inhibition in shaping them. In the locust LGMD neuron, the critical image cues for a directional response to an approaching object have been identified as an increase in the velocity of edge motion and an increase in the amount of edge (Simmons and Rind 1992). Either of these cues presented in isolation from each other induced a selective response in the neurons (Simmons and Rind 1992).

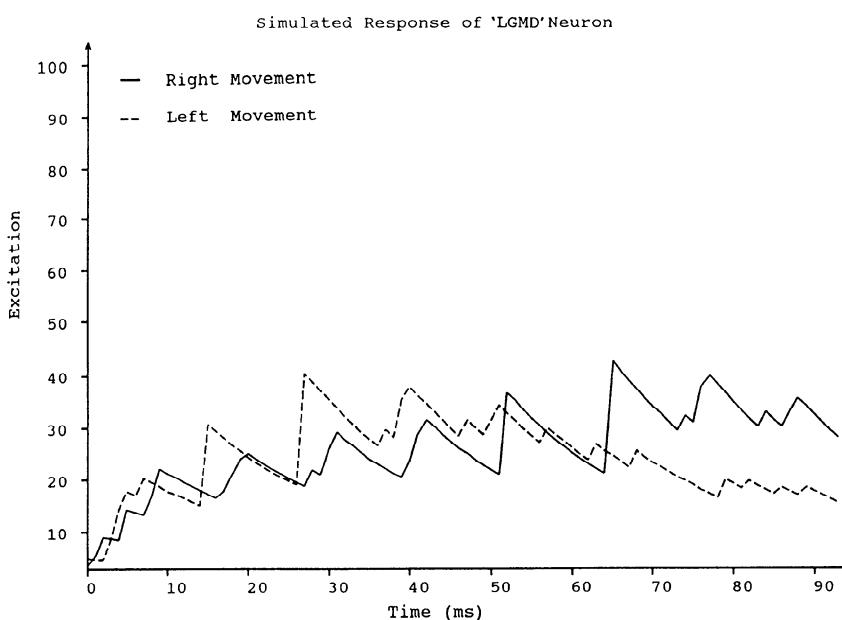


FIG. 6. Response of "LGMD" to rightward, vs. leftward, edge motion across eye. Edge that was 80 mm high and subtended 53 deg at eye moved at 0.75 m/s. Movement lasted 93 ms. Stimulus details as in Table 2.

When each of these cues is presented in isolation to the network "LGMD", the response, measured as peak excitation, is also selective (Fig. 7). The preferred stimuli for the "LGMD" are an increase in the velocity of edge motion (Fig. 7A) or an increase in edge extent (Fig. 7B). The importance of lateral inhibition in shaping this selectivity is revealed by examining the "LGMD" response when this inhibition is removed from the network. In the absence of any lateral inhibition, the selective response of the "LGMD" to edges that move with an increase in velocity or extent is either much reduced or abolished (Fig. 7). These results show that lateral inhibition is important in shaping the selective response in the "LGMD" and emphasize the match between the "LGMD" and the locust LGMD/DCMD neurons in the critical image cues for a directional response to approaching objects. These simulations establish that the "LGMD" responds in the same way as the locust LGMD/DCMD neurons to moving objects.

Network response to translation of single edges in the X-Y plane

The leading edge of a bar is made to move laterally to the right, across the eye at a constant 0.75 m/s, corresponding to an angular velocity at the eye of 287 deg/s (Fig. 8). As in most visual experiments, the network is allowed to adapt to the presence of the object on the screen before motion begins. Adaptation lasts for 66 ms, until excitation in the E units decayed completely, although there is still activity in I units (see Fig. 1). As the edge begins to move ($t = 0$ ms), excitation passes down the network to S units located in a position in the retinotopic array corresponding to the leading edge of the stimulus. Inhibition in I units increases and begins to extend in front of the moving edge, but at this stage, inhibition is not strong enough to stop any S units from reaching threshold and producing a spike. However, as the movement proceeds ($t = 20$ ms), the inhibition generated by the moving edge is strong enough to prevent some S units from firing when the edge passes over them. As the

simulation proceeds, inhibition continues to increase and spreads in front of the edge. Usually, some S units are prevented from reaching threshold by this inhibition and only at $t = 70$ ms do all the S units beneath the edge reach threshold. For the last 20 ms of the simulation, lateral inhibition again cuts back the excitation in the S units corresponding in position to the leading edge of the stimulus. After the edge has moved over them, excitation in E units decays rapidly (Tconst. of 12.3 ms) whereas excitation in I units (Tconst. of 55 ms) persists, creating a trail of inhibition. This figure shows the existence of a critical race for control of S unit activity between laterally extending inhibition and excitation passing retinotopically down the network.

Changing the velocity of edge motion allows the relative times of arrival of the laterally directed inhibition and the excitation at the S units to be altered. The responses of the network to edge velocities of 380 deg/s (1 m/s), 750 deg/s (1.5 m/s) and 1,150 deg/s (2.75 m/s) are shown in Fig. 9. When the activity in layers 2 and 3 of the network is examined at the end of the simulation, a gradual diminution in the effectiveness of the lateral inhibition is found as the velocity of edge motion increases (Fig. 9). Although the amount of inhibition has not changed, it is arriving at the S units of layer 3 after the edge-mediated excitation has arrived (the F unit is not activated by any of these translatory stimuli).

Network response to object approach

In this simulation, an object approaches the eye at 10 m/s on a collision trajectory (Fig. 10). At time 0 ms ($t = 0$), the network has adapted to the presence of the object's image on the photoreceptor array. Some activity is still present in the I units because these units have a longer time constant than the excitatory units on which adaptation time is based. As the object approach begins, the moving image edges generate excitatory responses in the P units of the input array. The excitation is passed on to layers 2 and 3 and the "LGMD" and at this stage is not checked by lateral inhibition because inhibition is delayed relative to excitation (2

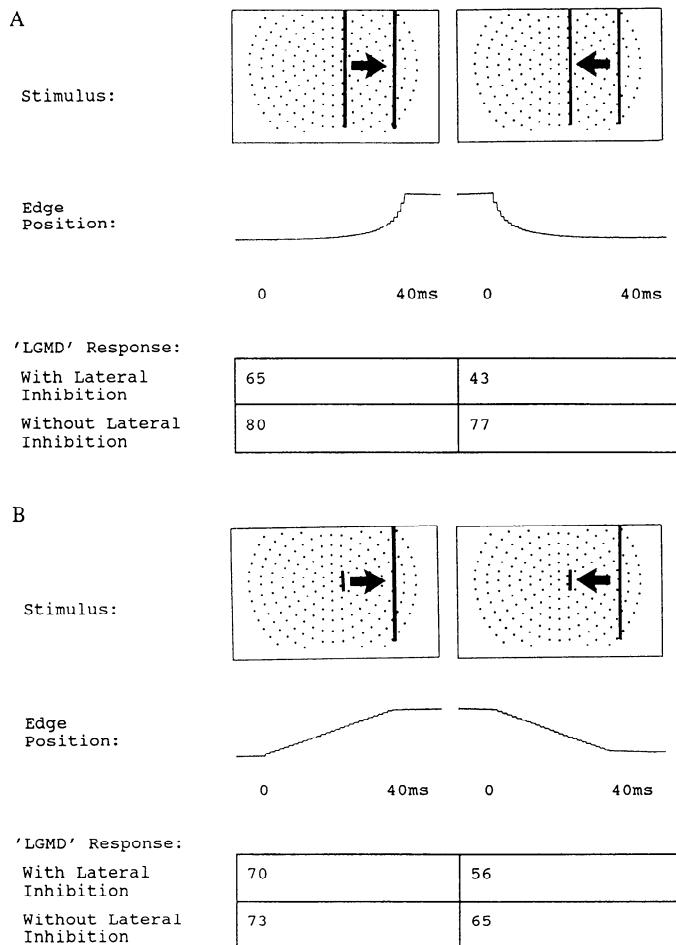


FIG. 7. Isolation of critical image cues for a directional response in "LGMD" and role of lateral inhibition in shaping them. Simulations were performed with either normal values for I unit-mediated lateral inhibition, as given in Table 2, or with no lateral inhibition (both nearest and next-nearest neighboring units set to 0.01%). "LGMD" response was measured as peak excitation level. A: a single edge moved across eye with same velocity as an edge of an object either directly approaching or receding from the eye (see Table 1). Edge length was constant throughout the movement. B: a single edge moved across eye, with same extent as an edge of an object directly approaching or receding from eye (see Table 1). Angular velocity was constant throughout the movement.

ms to nearest neighboring and 4 ms to next-nearest neighboring S units; see Table 2). As the approach proceeds ($t = 10$ ms), the lateral inhibition generated by the moving edges begins to spread out in layer 3 beyond the retinotopic position of the image and so beyond the edge-mediated excitation. At $t = 20$, the S units are not yet prevented from reaching threshold by this inhibition, although the strength of the inhibition is building up rapidly and between $t = 25$ and $t = 37$ ms, some S units are prevented from reaching threshold by the lateral inhibition. In the last stages of approach, the velocity of image edge motion continues to increase rapidly ($t = 38$), so that the edge-mediated excitation in layer 3 is able to escape the influence of the lateral inhibition (I unit activity). This allows excitation to build up very rapidly in layer 3 S units and consequently the "LGMD" (Figs. 2 and 10). In this phase of the object's approach, the large extent and rapid movement of the image edges also activate the feed-forward inhibition (F unit, *Fig. 2). This inhibition has a delay of 4.5 ms before it reaches the

"LGMD" so that, in this simulation, the cut back in response occurs after object approach has ceased. At the end of object approach a pool of strong inhibition is left in layer 2 in the wake of the rapidly moving image edges.

For approaching objects, increased velocity results in an increased number of S units in layer 3 reaching threshold. As the velocity of object motion increases, the object's image moves with sufficient speed over the eye that the E-unit-mediated excitation of S units is able to escape the suppressive influence of the laterally directed inhibition, carried by I units in layer 2. This is clearly seen in Fig. 11 where the activity present in the network at the ends of approaches of different speeds are shown. At the lowest velocity of object approach, the response of S units in layer 3 (Fig. 11, left, 4 m/s) is suppressed by the lateral inhibition (Fig. 11, right, 4 m/s). With approach velocities of 6 and 8 m/s, the excitation that passes down the network following edge motion escapes the suppressive influence of the lateral inhibition in the latter stages of object approach (Fig. 11). With a further increase in approach velocity ($v = 10-14$ m/s), the critical race, between excitation and lateral inhibition for control of the output of the S units in layer 3, is won by the excitation at successively earlier stages in the object approach until at 14 m/s very little suppressive influence of the lateral inhibition remains.

Network response to object recession

In this simulation, an object recedes from the eye at a velocity of 10 m/s (Fig. 12). As object recession is initiated, the moving image edges generate an excitatory response, which passes down the network and is not checked by any lateral inhibition. In this initial phase of the object's recession, the large extent and rapid movement of the image edges activate the feed-forward inhibition (F unit). This inhibition has a 4.5-ms delay before it reaches the "LGMD". In this simulation F unit inhibition acts at $t = 6$ ms to cut back excitation rapidly in the "LGMD" (*Fig. 2). At the same time, lateral inhibition extends in front of the edge-mediated excitation. Unlike the case for an approaching object, with a receding object the image edges move with ever decreasing velocity as the recession progresses, and this allows inhibition to prevent any excitation in the S units (Fig. 11). After $t = 10$ the edge-mediated excitation is progressively suppressed at layer 3, as excitation is overtaken by a growing area of inhibition ($t = 20, 30$, and 40 ms).

Movement of large objects at high velocities away from the eye lead to strong activation of the feed-forward inhibitory loop and a rapid and complete shut down of "LGMD" excitation (*Fig. 2, $v = 10-14$). Small objects moving at low velocity lead to weak activation of the feed-forward inhibitory loop and a partial or temporary shut down of excitation in the "LGMD" with residual network excitation in S units causing further "LGMD" excitation in the later stages of object recession (Figs. 2 and 3). This residual excitation after object recession is greatly accentuated in the absence of any lateral inhibition (see Fig. 13 below).

Importance of the critical race for directional selectivity

These experiments reveal the existence of a critical race between excitation, passing down the network, and inhibi-

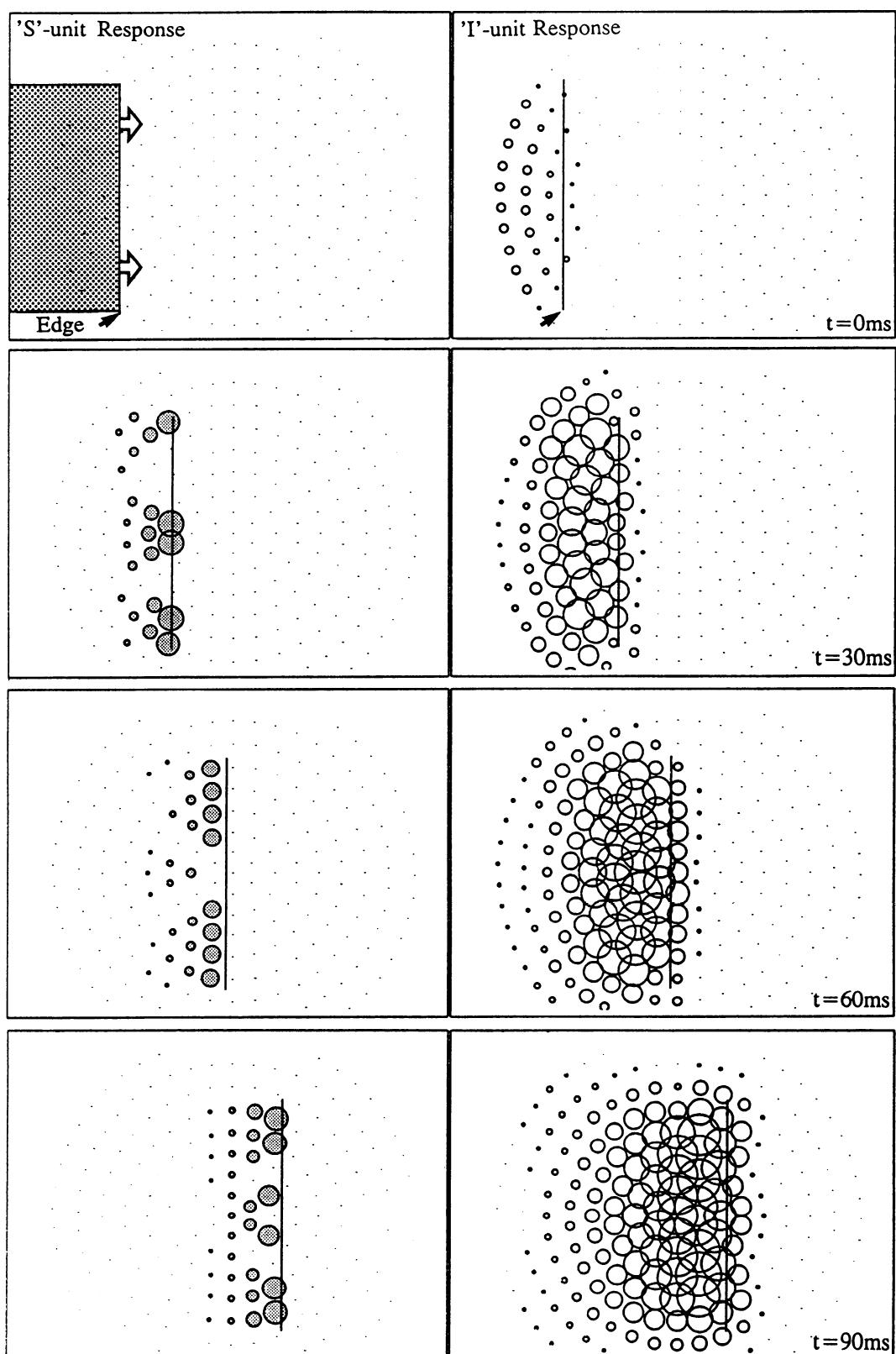


FIG. 8. Response of neural network "LGMD" to motion of an edge across eye. Edge that was 80 mm high and subtended 53 deg at eye moved at 0.75 m/s. Movement lasted 93 ms. Position of edge on array at 30-ms intervals during simulated motion is indicated by a solid line superimposed on the activity of layer 2, I units (Inhibition, *right*) and of layer 3, S units (level 3 response, *left*). I unit output onto layer 3 is shown.

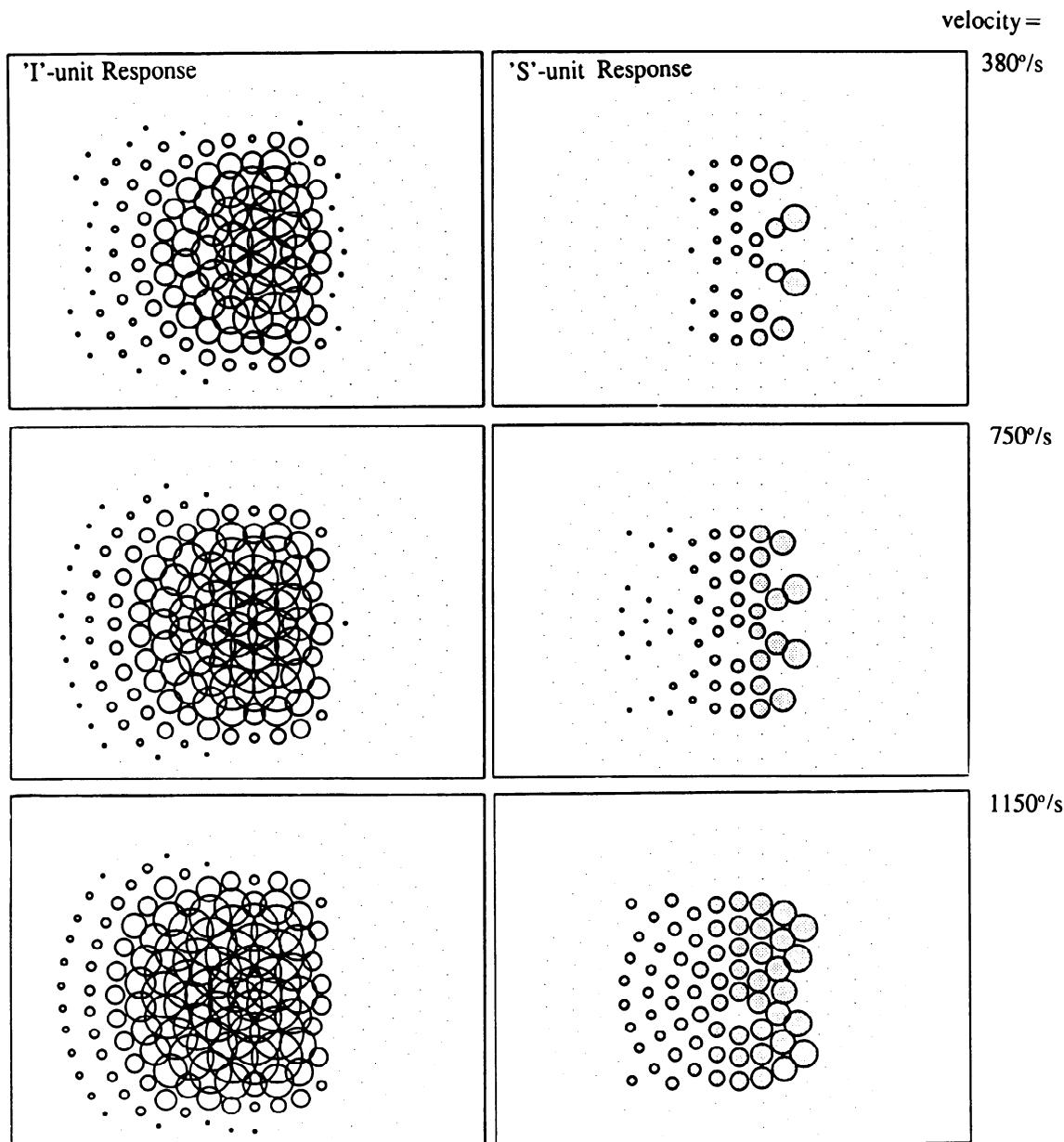


FIG. 9. Response of the network to movement of a single edge across eye at 1 of 3 velocities. Each snapshot shows activity in network in last 1 ms of simulation: *left* (level 3 response), S unit activity; *right* (inhibition), I unit output onto layer 3. Edge dimensions were as in Fig. 6.

tion passing laterally, for the selective response of the network. To test the importance of such a critical race, we alter first the strength and then the timing of lateral inhibition within the network and examine the response of the "LGMD" to approaching/receding objects and to translating edges (Fig. 13, A-E, stimulus details as in Table 1).

Reducing the strength of both the nearest neighbor and next-nearest neighbor I-unit-mediated lateral inhibition to 0 causes a small increase in the peak amplitude of the "LGMD" response in the final 9 ms of the simulated object approach (dotted line, Fig. 13A) but lead to a dramatic increase in "LGMD" excitation in the latter part of simulated object recession (dotted line, Fig. 13B), greatly reducing the directional selectivity of the network. With no lateral inhibition, the "LGMD" response to lateral movement of single edges is increased (Fig. 13C). The response of the

"LGMD" during the initial 12 ms of the simulation is not affected by the change in weight of lateral inhibition. Leftward and rightward movements are equally affected. Thus altering the strength, or timing, of lateral inhibition is found to alter the tuning of the "LGMD" for rapid motion of edges.

Decreasing the delay of the spread of I unit inhibition to nearest and next-nearest neighbor to 1 ms from 2 and 4 ms, respectively, reduces the "LGMD" response to both object approach and recession (dotted line, Fig. 13, D and E). The effect is to make it harder for excitation in S units to win the critical race. The usual peak in "LGMD" response to an approaching object is abolished because the edge-mediated excitation no longer overcomes the suppressive influence of the laterally spreading inhibition. By contrast, the response to receding objects is much less affected by reducing the

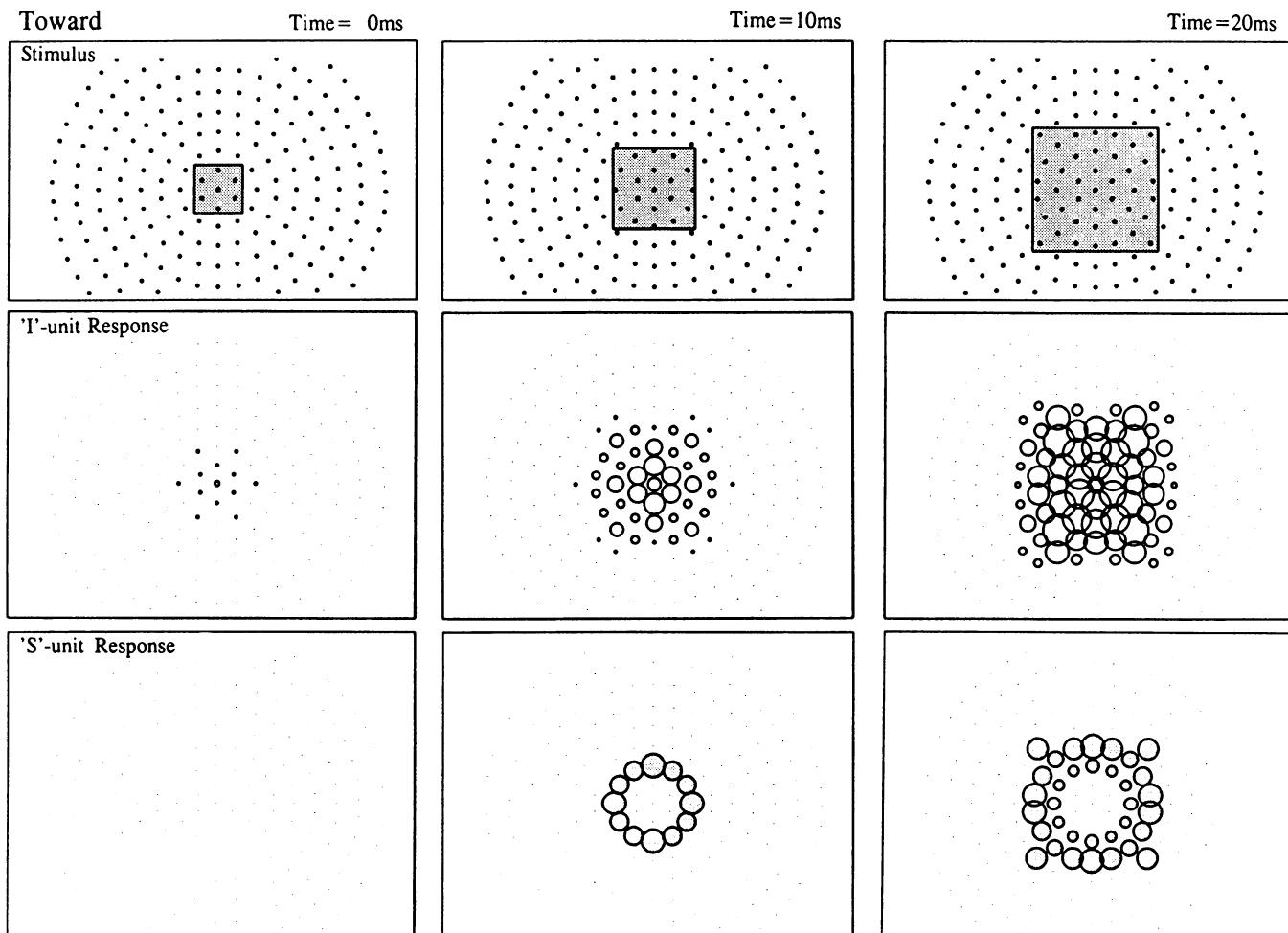


FIG. 10. Neural network response to an object 75×75 mm in size, approaching eye at a velocity of 10 m/s on a collision course. Initially object is 500 mm removed from "eye" and approaches to within 100 mm. Activity in layers 1–3 of network is shown at time 0, 10, 20, 37, 39, and 40 ms through the 40-ms simulation. Image of object remains on array throughout movement, although bottom edge moves out of figure at $t = 39$ ms. Activity of each unit within a layer was represented as a circle whose diameter reflects its level of excitation. Network was adapted to presence of image on eye, for 22 ms, before object motion began. Top (stimulus), image of approaching object mapped onto photoreceptor array (P units, layer 1); middle (inhibition), activity of lateral inhibitory units (I unit) at their output in layer 3; and bottom (level 3 response), activity of summing units (S units) in layer 3.

delay on the lateral spread of I unit inhibition. As before, the "LGMD" responds to object recession with a brief, intense peak of activity at the beginning of object recession but the amplitude of the response is slightly reduced (dotted line, Fig. 13E).

Removing F unit mediated feed-forward inhibition prolongs "LGMD" excitation in response to both object approach and object recession. The response to object approach is prolonged, after the end of the stimulus, and the response to object recession is now maintained throughout movement of the image (Fig. 13F). In the absence of F unit activity, the "LGMD" response to receding objects declines gradually as activity in S units decays and no further S unit activation occurs due to the spread of lateral inhibition into the areas where the image edges now fall.

DISCUSSION

The neural network based on the input organization of the LGMD neuron in the locust visual system responds directionally when challenged with approaching and receding ob-

jects. The directionality is maintained with objects of various sizes and approach velocities and the network is tuned to direct approach and shows no selectivity for different directions of translatory motion across the eye. The critical image cues for a selective response to object approach by the "LGMD" are growing edges, or edges that move with increasing velocity over the eye. The network responds in the same way as the locust LGMD neuron and meets the criteria set out as a good challenge of the correspondence between network and neuron. The network allows the following conclusions to be drawn about the mechanisms shaping the selective response of the LGMD neuron to approaching objects.

Inhibition and its role in directional selectivity

The critical image cues for a selective response to object approach by the "LGMD" are edges that change in extent or in velocity as they move (Fig. 7). Lateral inhibition is crucial to the selectivity of the "LGMD" and the selective response is abolished or else much reduced if lateral inhibi-

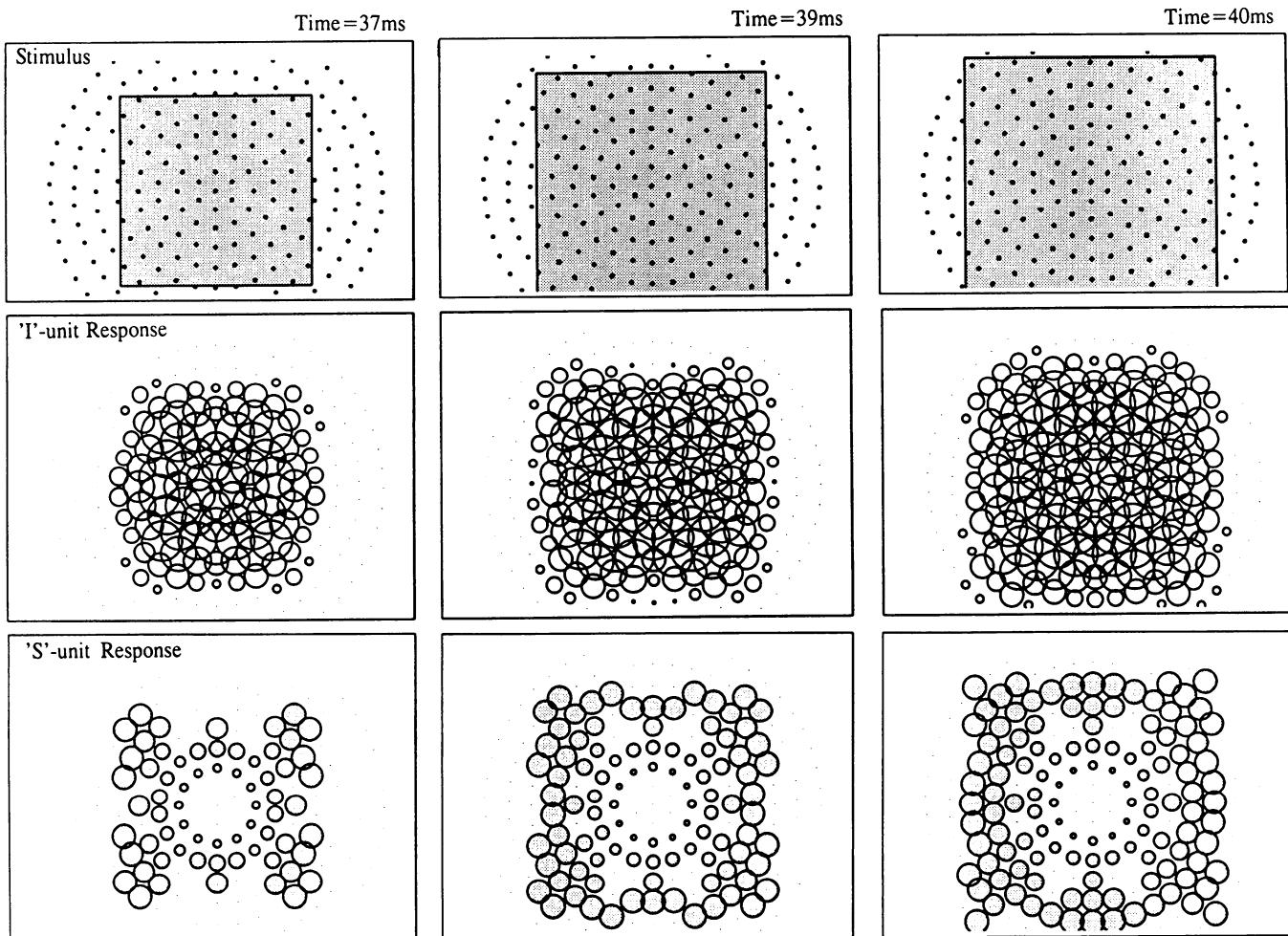


FIG. 10. (continued)

tion is taken out of the network (Fig. 7). We conclude that lateral inhibition in the neuronal network for the locust LGMD also underlies the experimentally observed critical image cues for its directional response. Lateral inhibition is a prominent feature of the receptive field organization of the locust LGMD neuron, and one function already suggested is to protect the decrement prone small-field excitatory afferents from habituation (Rowell et al. 1977). In the neural network, lateral inhibition enhances the selective response to approaching objects and, in conjunction with other processes, tunes the network to objects approaching on collision trajectories: as an object approaches the eye of the network, there is a rapid buildup of excitation in the output element of the network, the "LGMD". Essential to this buildup of excitation in the "LGMD" is a critical race between excitation passing down the network and inhibition directed laterally in layers 2 and 3 of the network. The conduction delay of the lateral inhibition determines at which speed of approach, and at which point in the approach, the race between excitation and inhibition for control of the output of layer 3 will be won by excitation. Directional selectivity is enhanced greatly by feed-forward inhibition. Whereas the feed-forward loop is activated at the end of object approach, truncating the excitatory "LGMD" response to approaching objects after approach has occurred, the feed-forward loop is activated at the initiation of object recession truncating the

"LGMD" response during object movement. A receding object evokes only a brief, intense peak of activity, with a rising phase of 3–5 ms, that then is cut back by feed-forward inhibition. Without the feed-forward loop, the initial response of the "LGMD" to object recession declines slowly, with a time course dependant on the time constant of the S units in layer 3 of the neural network (Fig. 13F). As recession progresses, lateral inhibition prevents activation of further S units, because, unlike object approach, both edge extent and velocity are ever decreasing.

Inhibition strength and its role in directional selectivity

The strengths of inhibition used in the model are very modest and we were particularly cautious about overestimating the strength of the lateral inhibition because this has been a problem with theoretical studies of the mechanism of directional selectivity in the past. For example, Koch and Poggio (1983), in their model of the inhibitory interaction responsible for generating directional selectivity in the cat cortex, predicted that a measurable conductance increase should accompany shunting inhibition during motion in the nonpreferred direction. However, Douglas, Martin, Whitteridge, and coworkers (1988, 1991) examined the synaptic interactions underlying directional selectivity by making intracellular recordings from directionally selective cortical

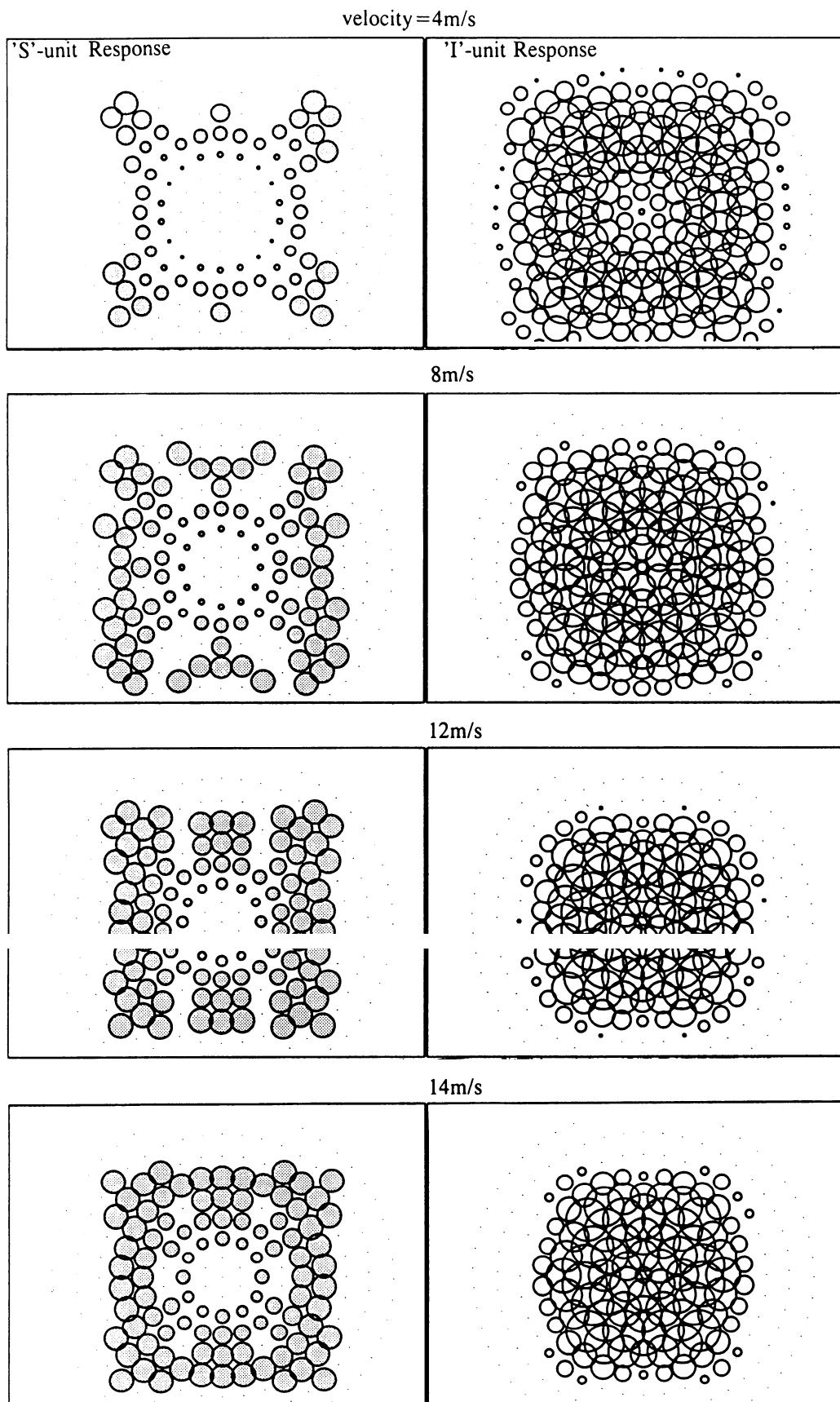


FIG. 11. Neural network response to an object approaching eye on a collision course. Each snapshot shows activity in network in last millisecond of simulation. Approach velocities of 4, 8, 12, and 14 m/s are shown. At each velocity, activity of S units in layer 3 is shown on *left* (level 3 response) and output activity of I units from layer 2 is shown on *right* (inhibition).

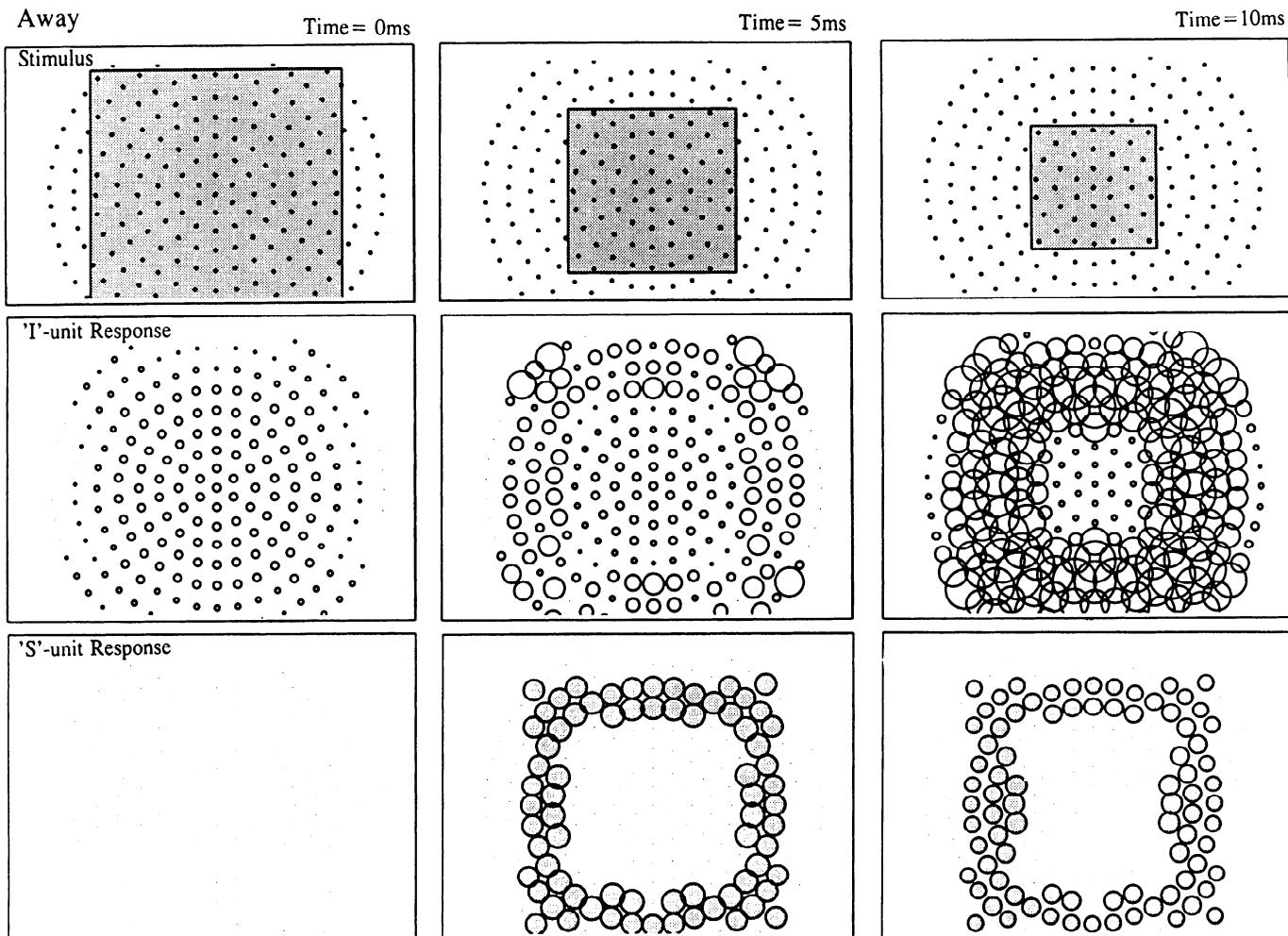


FIG. 12. Neural network response to an object 75 × 75 mm in size directly receding from eye at a velocity of 10 m/s. Object is initially 100 mm from eye and recedes to 500 mm. Stimulus conditions and network parameters were as in Tables 1 and 2, except that course of object was reversed. Network was adapted to presence of image on eye, for 22 ms, before object motion began. Activity in layers 1–3 of the network is shown at time 0, 5, 10, 20, 30, and 40 ms through 40-ms simulation. Top (stimulus), image of approaching object mapped onto photoreceptor array (P units, layer 1); middle (inhibition), activity of lateral inhibitory units (I unit) at their output in layer 3; and bottom (level 3 response), activity of summing units (S units) in layer 3.

neurons and failed to reveal conductance changes of the order of magnitude predicted by Koch and Poggio (1983, 1985). In their simulation of the “canonical” circuit underlying directional selectivity in the cat visual cortex, Douglas and Martin (1991) found that the relative timing of the excitation entering the circuit and the inhibition generated within the circuit was the critical feature determining whether inhibition or excitation will predominate the response. In the preferred direction, the excitatory input arrives first and is able to produce strong cortical re-excitation, which cannot be inhibited despite the strong inhibition that this excitation also evokes.

In the “LGMD” neural network, the maximum possible lateral inhibition directed at an S unit in layer 3 was 2.4 times the excitation delivered from an E unit in layer 2, a level of inhibition that was only reached with simultaneous activation of all 6 S units neighboring and 12 next-neighboring I units such as would occur during a whole-field light on or off stimulus. The synaptic gain for transmission from I unit to each of the 6 nearest neighboring S units was given a value of 0.284, whereas that to the 12 next-nearest

neighboring S units was 0.058. For comparison, the inhibitory synapse between photoreceptors and laminar monopolar cells in the fly retina has a maximum gain of -6 (Laughlin et al. 1987), and the excitatory synapse between the locust LGMD and DCMD neurons has a gain of plus 1.2 (Rind 1984). In both the LGMD and “LGMD”, the feed-forward inhibitory loop was able to suppress completely an ongoing response (O’Shea and Rowell 1975) (Figs. 2–4). The gain of this loop in the neural network was variable, increasing with the number of activated photoreceptors. The feed-forward loop in both the locust and the neural network LGMDs exhibited the computational features of proximal neuronal inhibition, whereas the effects of lateral inhibition more closely resembled those of distal neuronal inhibition (Vu and Krasne 1992).

In the neural network, a conservative estimation of the extent of lateral inhibition was employed, extending it only to nearest and next-nearest neighbors. This resulted in a spread of inhibition over a visual angle of roughly 12 deg. Rowell et al. (1977) estimate its spread in the locust LGMD to be ≤ 20 deg. Initially, two configurations of the neural

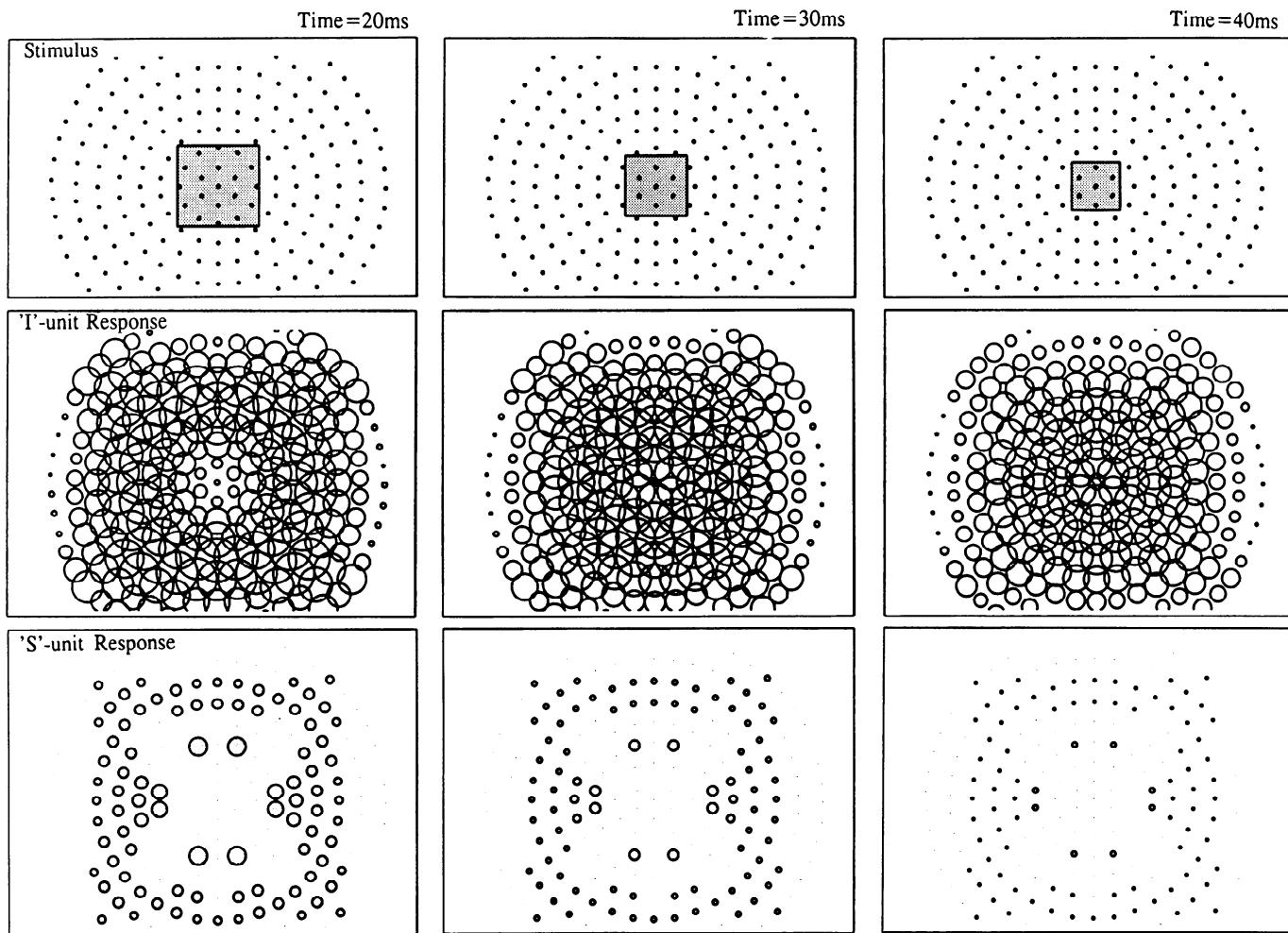


FIG. 12. (continued)

network were created. In the first, the lateral spread of inhibition was delayed relative to the excitation passing downward through the layers of the network: 2 ms to the nearest and 4 ms to the next nearest neighbors. In the second, lateral inhibition was not delayed (Fig. 13, *D* and *E*). No direct experimental evidence is available to distinguish between these two alternatives, although intracellular recordings from the LGMD verified the responses predicted by the first configuration of the network (F. C. Rind, unpublished observations) and all the results shown in this paper use this version. These delays would be consistent with a conduction delay: in *Limulus* eccentric cells the lateral processes that mediate lateral inhibition are much finer than those conducting information centrally (Fahrenbach 1985) and so lateral inhibition travels relatively slowly. In the locust, synaptic delays between some neurons are as short as 1 ms and thus too rapid to be solely responsible for a 2- to 4-ms delay (Rind 1984), however, both inhibitory and excitatory synapses between ocellar neurons are known to have delays of 3–4 ms (Simmons 1982). Anatomic evidence shows that these ocellar synapses are monosynaptic (Littlewood and Simmons 1992). In the “canonical” circuit in cat cortex, the inhibition is thought to be mediated by GABA_B receptors and outlasts the excitatory currents in the same neurons (Douglas and Martin 1991). The slow onset and decay of the inhibition also is seen in the neurons of the tiger salamander retina

and involves GABA_B and glycine receptors (Frumkes et al. 1981; Maguire et al. 1989; Werblin 1991). GABA_B receptors with similar response features are known in insects and these were used as a guide to the properties of the I units responsible for lateral inhibition in the present neural network (Bai and Sattelle 1995). The slow onset of inhibition may combine with lateral conduction delays and a synaptic delay to produce the 2- to 4-ms delay incorporated into the lateral spread of inhibition within the neural network. GABAergic neurons are thought to be present in the insect medulla and lobula and have been implicated in the shunting inhibition mediating directional selectivity in the fly (Bültöff and Bültöff 1987), however, the pattern of GABA reactivity in locust optic lobes and the involvement of GABA_B receptors is not known.

Neurons and networks signalling motion in depth using monocular cues

In humans, a compelling impression that an object is moving in depth is given when its magnification on the retina is increased (Wheatstone 1852). Size change neurons or psychophysical channels have been described in a wide range of animals including humans (Cynader and Regan 1978; Hong and Regan 1989; Regan and Beverley 1978; Tanaka et al. 1989; Wang and Frost 1992; Zeki 1974). In

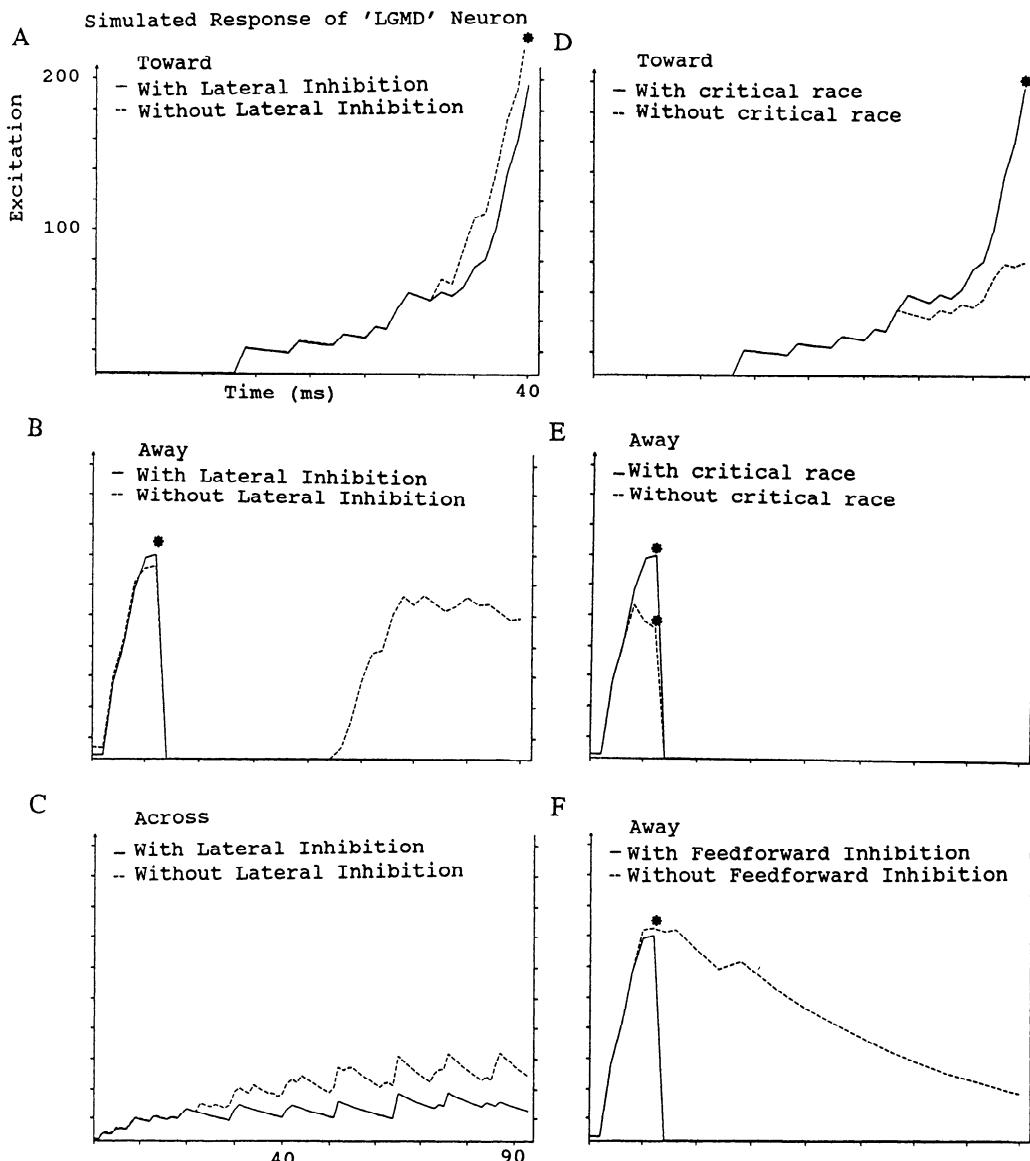


FIG. 13. Effects of changing network parameters on response of "LGMD". Role of inhibition in response to objects that move toward, away from, or across eye (stimuli as in Table 1). A–C: with and without lateral inhibition. D and E: with and without a race between excitation and lateral inhibition (without a race: delay on inhibition <1 ms). F: with and without feed-forward inhibition.

those size change neurons that have been studied to date, divergent motion of image edges (or other image features) has been a critical image cue for a directional response (Regan and Cynader 1979; Zeki 1974). Liaw and Arbib (1993) have developed a neural network that mimics the direction selective avoidance response shown by anurans to approaching objects. The sensitivity of the network to radial edge expansions and to the net receptor dimming is modeled on the responses of neurons in the frog tectum (T3), which are direction selective for object motion in depth (Grüsser and Grüsser-Cornehls 1976). In the network, each T3 neuron receives inputs from photoreceptors looking out over a 40×40 -deg patch. The detection of radial edge expansion is achieved by increasing the synaptic weighting toward the periphery of each T3's receptive field. As a consequence, maximal activation of the network is only achieved if the object edges expand within the 40×40 deg extent of each T3 receptive field. This means that the response is not inde-

pendent of object size or contrast and that time to collision cannot be signalled unambiguously. In their simulations, object distance is not calculated by the network but was measured independently and added subsequently to allow appropriate reactions to be timed. Even with these limitations, the network has been effective in mimicking frog approach/avoidance behavior in response to objects moving toward the animal.

As the present network is the first example incorporating the receptive field organization of an identified neuron, which is selective for motion in depth, it is not possible to determine the generality of the neuronal interactions involved. However, the ability of animals to estimate time to collision with either a rapidly approaching object or surface using auditory or visual cues derived from one eye is well documented behaviorally. Lee (1980) has described a variable tau ($\tau = \text{image size}/\text{rate of change in image size}$) that allows the time to contact with an approaching object to be

determined without first measuring its approach velocity and distance. Tau (τ) is thought to be used to time behavior by plunge diving gannets (Lee and Reddish 1981), landing flies (Wagner 1982), landing pigeons (Lee et al. 1993) and bats navigating around obstacles or through narrow openings (Lee et al. 1992). These findings suggest the generality of such a strategy and emphasize the importance of any solution in terms of the neuronal processing involved. Wang and Frost (1992) described neurons in the nucleus rotundus of the pigeon brain that responded selectively to images of an object approaching the bird on a collision course. The looming sensitive neurons used monocular cues to signal a constant time to collision of 1 s, irrespective of object size or approach velocity. Wang and Frost concluded that these neurons were involved in initiating and controlling the pigeon's avoidance behavior to such looming objects. These observations provide evidence that there are mechanisms in the pigeon visual system capable of extracting tau (τ).

The neural network described in this paper was based on the input organization of the LGMD neuron, which has been shaped by natural selection over millions of years, particularly as the pathway is thought to be crucial to individual survival, functioning in escaping imminent predation (Rind and Simmons 1992). The network, and the pathway that inspired it, both gave a rapid and robust response to approaching objects, regardless of whether the object was lighter or darker than the background. The response of the system increased rapidly as an object approached. Object collision was signaled independently of approach trajectory as there was no hard-wired system for detecting the pattern of radial edge expansion that accompanied object approach. The network was found to be tuned to detect the time-varying features of the image of an approaching object on a collision course.

In the "LGMD", both lateral inhibition and feed-forward inhibition underlie selectivity for objects rapidly approaching on a collision course. Removing or altering the timing of either lateral inhibition or feed-forward inhibition reduced the selective response to approaching objects (Fig. 13). The selectivity of the network and by analogy the LGMD neuron is due to the timing of the critical race between the excitation passing down the network and both forward and laterally directed inhibition. For excitation to dominate, excitation must arrive before laterally extending inhibition and before feed-forward inhibition is initiated. Feed-forward inhibition is switched on after the stimulus movement has ceased for an approaching object and during the movement for a receding one. The model allowed the role of these processes in the selective responses of the locust neurons to be studied.

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NOTE ADDED IN PROOF

The finding that Lobula Giant Movement Detector (LGMD) excitation builds up throughout object approach directly contradicts the findings of Hatsopoulos et al. (Hatsopoulos, N., Gabbiani, F., and Laurent, G. Elementary computation of object approach by a widefield visual neuron *Science Wash. DC* 270: 1000–1003, 1995).

A probable explanation for this is that their visual stimuli were not adequate to excite the LGMD at the end of object approach when the rate of image change is high. Their experiments plot the failure of their visual stimulus to excite the LGMD rather than any response of the neuron. Consistent with this, Simmons and Rind (1992) report that edge jumps of $>5^\circ$ at the eye result in a rapid decline in LGMD excitation.

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