Motion Detectors in the Locust Visual System: From Biology to Robot Sensors

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ABSTRACT Motion detectors in the locust optic lobe and brain fall into two categories: neurones that respond selectively to approaching vs. receding objects and neurones that respond selectively to a particular pattern of image motion over a substantial part of the eye, generated by the locust’s own movements through its environment. Neurones from the two categories can be differentiated on the basis of their response to motion at a constant velocity at a fixed distance from the locust: neurones of the first category respond equally well to motion in any direction whereas neurones in the second category respond selectively to one preferred direction of motion. Several of the motion detectors of the first category, responding to approaching objects, share the same input organisation, suggesting that it is important in generating a tuning for approaching objects. Anatomical, physiological, and modelling studies have revealed how the selectivity of the response is generated. The selectivity arises as a result of a critical race between excitation, generated when image edges move out over the eye and delayed inhibition, generated by the same edge movements. For excitation to build up, the velocity and extent of edge motion over the eye must increase rapidly. The ultrastructure of the afferent inputs onto the dendrites of collision sensitive neurones reveals a possible substrate for the interaction between excitation and inhibition. This interpretation is supported by both physiological and immunocytochemical evidence. The input organisation of these neurones has been incorporated into the control structure of a small mobile robot, which successfully avoids collisions with looming objects. The ecological role of motion detectors of the second category that respond to image motion over a substantial part of the visual field, is discussed as is the input organisation that generates this selective response. The broad tuning of these neurones, particularly at low velocities (<0.02°/s), suggests they may have a role in navigation during migratory flights at altitude. By contrast, their optimum tuning to high-image velocities suggests these motion detectors are adapted for use in a fast flying insect, which does not spend significant time hovering. Microsc. Res. Tech. 56:256–269, 2002.

INTRODUCTION
Locusts exhibit a wide variety of visually guided behaviours, many controlled by neurones signalling motion. For example, locusts use motion detecting visual neurones to avoid collisions in flight (Robertson and Johnson, 1993a,b), maintain a straight flight path (Baader et al., 1992; Hensler and Rowell, 1990; Lorez, 1995; Miall, 1990), adjust forward flight speed (Preiss and Gewecke, 1991; Riley et al., 1988; Thorson, 1966), hide or escape from predators (Hassenstein and Hustert, 1999; Judge and Rind, 1997) and judge distance to a nearby object (Collett and Paterson, 1991; Sobel, 1990). Locusts occupy a particular ecological niche and their motion detectors reflect this: the largest motion detectors in the locust respond best to rapidly approaching objects, by contrast the largest motion detectors in the fly respond best to image motion generated by the fly’s own deviations from a straight flight path (Franceschini et al., 1992). Locusts also make long migratory flights in dense swarms, travelling at heights of up to 2 km where any motion over the eyes will be extremely slow (Uvarov, 1977). Since the 1960s, it has been known that locusts are exquisitely sensitive to motion over the eye, with behavioural responses to movements as slow as 0.004°/s (Riley et al., 1988; Thorson, 1966). Correspondingly, some directionally selective motion detecting neurones recorded from the locust visual system are able to signal very low image drift speeds (Kien, 1974; Osorio, 1986; Riley et al., 1988).

The compound eye in the locust (Fig. 1) consists of around 8,500 facets each with its own lens and each viewing an area of space separated by 1.25° from the visual axis of its neighbour (Horridge, 1978; Wilson, 1975; Wilson et al., 1978). Beneath each facet are eight light-gathering photoreceptors, all of which contribute to a single fused rhabdome viewing the same region in space. In the locust, the angular sensitivity half-width of a light-adapted photoreceptor is 1.5° (Wilson et al., 1978). Six of these photoreceptors project into the first neuropile in the optic lobe, the lamina, while the remaining two project...
through the lamina into the medulla, preserving their precise retinotopic mapping as they do so (Wilson et al., 1978). It is in the medulla that small-field neurones that respond specifically to motion rather than flickering stimuli are first found (James and Osorio, 1996; Osorio, 1986, 1991), so it is likely that the first motion computation is made in the medulla. However, the small size of these neurones has made recording from them difficult. The best-characterised motion-detecting neurones in the locust occur in the third optic neuropile, the lobula where they project over substantial portions of the visual field and sum input over a wide area (Gewecke et al, 1990; Gewecke and Hou, 1993; O'Shea and Williams, 1974; Rind, 1987, 1990a,b). These motion detecting neurones fall into two categories: ones that respond equally well to any motion at a fixed distance from the locust (XY plane in Fig. 2) and ones that respond selectively to particular directions of motion in the XY plane. These two types of motion detectors contribute to very different behaviours in the locust. Recently, some of the neurones that respond non-directionally to motion at a fixed distance from the locust have been found to respond selectively when that motion is toward the locust (see Rind and Simmons, 1999, for a recent review).

**VISUAL NEURONES SIGNALLING MOTION IN DEPTH**

**General Features of the Neurones**

Several insects including locusts have motion detectors that respond equally vigorously to movement of an object in any direction when motion is at a fixed distance from the animal (Rind, 1987; Rowell, 1971; Srinivasan et al., 1993). Two of the most studied, and largest neurones in the locust nervous system, the lobula giant movement detector (LGMD 1), and its postsynaptic partner, the descending contralateral movement detector (DCMD), respond in this way, responding best to novel motion of a small dark object anywhere in the receptive field of one eye (Kilmann et al., 1999; O'Shea and Williams, 1974; Rind, 1984; Rowell, 1971). The DCMD neurone is excited by the LGMD 1 and follows spikes in it one for one at frequencies in excess of 400 Hz (Rind, 1984). Anatomically, the synapse between the LGMD 1 and the DCMD consists of upwards of 2,250 contacts (Kilmann et al., 1999). The DCMD projects down the nerve cord into the thorax and makes output connections to leg and flight motoneurones and interneurones that are consistent with a role in escape jumps and avoidance manoeuvres in flight (Burrows and Rowell, 1973; Gynther and Pearson, 1989; Rind, 1984; Robertson and Johnson 1993a,b; Simmons, 1980; reviewed in Rind and Simmons, 1999). This was thought to be the whole picture, a small moving object leading to an escape jump or steering reaction during flight, until several classes of motion-sensitive visual neurones from the locust optic lobe and protocerebrum were identified that had the same non-directional response to motion in the XY-plane as the LGMD 1/DCMD neurones and protocerebrum were identified that had the same non-directional response to motion in the XY-plane of the locust nervous system.
the LGMD 1. Star Wars contained many images of approaching objects and this, coupled with a thorough analysis, revealed that the LGMD 1 responded directionally to approaching objects (Rind and Simmons, 1992; Simmons and Rind, 1992). Like the LGMD 1, other known non-directional motion detecting neurones also demonstrated a selective response to approaching objects (Gewecke et al., 1990; Gewecke and Hou, 1993; Rind, 1996; Simmons and Rind, 1998). The input organisation exemplified by the LGMD 1 is now known to subserve a more fundamental role than was first appreciated, the input organisation creates a selectivity for motion in depth (Gewecke et al., 1990; Gewecke and Hou, 1993; Rind, 1987). The anatomy and synaptic organisation of the LGMD 1 and 2 neurones are addressed in the next section.

Fig. 3. Morphology of the LGMD 1 and 2 neurones and their input organisation. A: The LGMD 1 and the LGMD 2 have been stained with hexaminecobaltic chloride and viewed from behind. The main dendritic branches of the LGMD 1 and 2 occur in the lobula area of the optic lobe, and an axon projects into the lateral protocerebral area of the brain. B: Electron micrograph showing the paired arrangement of afferent inputs onto the LGMD 1 dendritic fan (asterisk) in the distal lobula. Each afferent process synapses with its neighbour and the LGMD 1. A small LGMD profile (asterisk) is surrounded by, and postsynaptic to, five afferent processes (numbered). C: Intracellular recordings from the locust LGMD 1 to show lateral inhibition. Recordings were made from the dendritic fan of the locust LGMD 1 in the lobula, while the locust viewed a screen on which two vertical bars moved laterally, posteriorly over the eye. The timing of the movements are indicated as horizontal lines under the intracellular recording. Movement of the right (R) bar alone caused vigorous excitation of the LGMD 1 (top), which was reduced if the left (L) bar moved before the right (R) one (middle). Following movement of the left (L) bar alone, no IPSPs were recorded in the LGMD 1, even when it was depolarised by injected current (4.0 nA) to accentuate any IPSPs, indicating that the inhibitory effect occurred presynaptically to the LGMD 1 (modified after Rind and Simmons, 1998.)
ANATOMY AND SYNAPTIC INPUT ORGANISATION

The best-characterised of these neurones are the LGMD 1 and 2 with their fan-like dendritic arborisations in the optic lobe, within the distal layer of the lobula (Fig. 3A). The dendrites of the LGMD 2 lie more superficially than those of the LGMD 1, nearer the posterior surface of the optic lobe. The LGMD 1 has additional dendritic sub-branches, compared to the LGMD 2, and both neurones project into the brain to the lateral protocerebrum. Like all the known neurones of this class, the LGMD 1 and 2 represent parallel processing streams with no synaptic interconnections at this level (Rind, 1987). Their similar responses are conferred by a shared input organisation (Simmons and Rind, 1997). The synaptic inputs to the LGMD 1 are thought to be as follows: the LGMD 1 receives excitatory inputs from a retinotopic array of small-field, spiking neurones excited transiently by changes in illumination (O’Shea and Rowell, 1976). Synaptic transmission decrements between these afferents and the LGMD 1 with repetitive stimulation (O’Shea and Rowell, 1975, 1976; Rowell et al., 1977). Strong lateral inhibitory interactions occur between these small-field neurones (Edwards, 1982; O’Shea and Rowell, 1975; Pinter, 1977; Rind and Simmons, 1998, 1999) and conduction delays occur as the inhibition spreads laterally (Edwards, 1982; Pinter, 1977). Inhibitory inputs on the LGMD 1 are activated by sudden or intense large-field stimuli such as a flash of light (Palka, 1967). The inhibitory inputs have longer latencies than the excitatory PSPs evoked by the same instantaneous stimulus (range: 5–15 ms; Edwards, 1982; Pinter, 1977). Over their surface in the lobula, the dendrites of both the LGMD 1 and 2 receive many synapses from afferent processes (Rind and Leitinger, 2000; Rind and Simmons, 1999). These afferent inputs occur at high density and have a characteristic configuration, particularly when the section plane passes at right angles to the long axis of the presynaptic density (Fig. 3B). It is clear that there are two post-synaptic elements at each synapse, the LGMD 1 or 2 (in Fig. 3B) and the neighbouring afferent process. The synapses are at such high densities that around the many small LGMD processes (<300 nm) they characteristically form cartwheel-like structures consisting of 3–7 afferent processes all synapsing with the neighbouring afferent process and the LGMD 1 or 2 (Fig. 3B). Intracellular recordings from the LGMD neurones (Fig. 3C) reveal no excitatory interactions between neighbouring afferents: motion of a small dark bar causes a brief burst of action potentials in the LGMD 1. When bar movement is preceded by movement of a nearby bar, the response to the movement of this previously effective stimulus is reduced. The inhibitory interaction occurs presynaptically to the LGMD 1 as no IPSPs are visible in the LGMD 1 during the suppression even when the LGMD 1 has been depolarised to make them more visible (Fig. 3C, bottom trace). This and other observations suggest that the interaction between afferents at the surface of the LGMD is inhibitory, in addition to exciting the LGMD 1 or 2 (Rind and Simmons, 1998). These synapses are ideally placed for such presynaptic inhibition as the receptors must be very close to the site of neurotransmitter release. Recently histochemical and immunohistochemical evidence has indicated that acetylcholine is a strong candidate as the neurotransmitter at the afferent synapses (Rind and Leitinger, 2000; Rind and Simmons, 1998). This raises the possibility that the dual effects of excitation onto the LGMD 1 and 2 vs. lateral inhibition between afferents, is due to the differing properties of the receptors for the same neurotransmitter on the two postsynaptic neurones. Excitation could be produced via fast nicotinic receptors at the postsynaptic membrane of the LGMD 1 or 2 whereas lateral inhibition could be produced via slower muscarinic receptors on the afferent process. Inhibitory muscarinic receptors have been found in insects but their temporal properties are not well known (Trimmer, 1995). The significance of such a synaptic arrangement for the response of the LGMD 1 and 2 neurones for approaching objects is discussed later (see Input Organisation of the LGMD Contributing to Its Directional Responses: Modelling and Robotic Studies).

PHYSIOLOGICAL RESPONSES TO OBJECT MOTION

Responses to Approaching Objects

At least two of the motion sensitive neurones in the lobula, identified as nondirectional when presented with motion in the XY-plane, respond directionally when challenged with motion in the Z direction, approaching the eye (see Fig. 4) (Gabbiani et al, 1999; Hatsopoulos et al, 1995; Rind and Simmons, 1992,
1997; Simmons and Rind, 1992, 1997). The LGMD 1 and 2 respond best to approaching objects over a range of speed from 0.25 to 12.0 m/s. The response of the LGMD 1 and 2 neurones to a rapidly approaching object (approach velocity >1 m/s) on a collision trajectory usually builds up throughout object approach, reaching a peak only after a collision would have occurred (Gray et al., 2001; Judge and Rind, 1997; Rind and Simmons, 1992, 1997; Rind, 1996; Robertson and Gray, 1997; Simmons and Rind, 1992, 1997). The response to a rapidly approaching object is actively curtailed by IPSPs, which are usually recorded after the approach has ceased and collision would have occurred. The peak in excitation is graded in intensity, with the strongest response given to faster velocities of approach, with a maximum at around 5 m/s, and to larger sized objects (Judge and Rind, 1997; Rind, 1996; Simmons and Rind, 1992, 1997). When a computer screen is used to stimulate the LGMD 1 and 2 neurones, care must be taken to ensure that image edge motion should be smooth and occur over near neighbouring retinotopic units (Rind and Simmons, 1997; Simmons and Rind, 1992). This contrasts with the responses recorded from the DCMD by Gabbiani et al. (1998, 1999, 2001) who have consistently found that the response declines before the end of object approach. The decline, which generates a peak in the DCMD spike train, is not observed when high approach velocities (6–10 m/s) or when the smallest object size (12 cm in diameter) are simulated. The LGMD 1 and the DCMD are subject to modulatory influences and these may contribute to the differences in response pattern observed (Rowell and O’Shea, 1975; Stern et al., 1995; Zaretski, 1982). Recently, Gray et al (2001) recorded DCMD responses that followed object approach throughout the movement, with a peak DCMD firing frequency of 240–320 Hz, much higher than that recorded by Gabbiani et al. (1998).

### Responses to Receding Objects and Critical Image Cues for a Selective Response

The response of the LGMD 1 and 2 neurones to an object receding (Fig. 4A–C) is very brief by comparison with that to the same object approaching; there is an initial intense excitation but that is rapidly truncated by a barrage of IPSPs (Rind, 1996; Simmons and Rind, 1997). The whole response lasts only 10–20 ms and is over before recession has stopped. The LGMD 1 and 2 neurones can discriminate between approaching and receding objects using image cues derived from one eye (Rind and Simmons 1992; Simmons and Rind, 1992, 1997). There are two critical image cues for the selective response of the LGMD 1 and 2 neurones to approaching objects: 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 (Fig. 5). Addition of either of these cues to edge motion (Fig. 5B) results in a selective response, with increasing velocity of edge motion (Fig. 5B) or increasing amount of edge (Fig. 5C) eliciting the strongest response. The neurones both respond vigorously to motion of an edge at a constant high velocity but the response is very brief; for the response to follow the movement throughout its duration the edge must move with an increasing velocity over the eye (Simmons and Rind, 1992, 1998). The response does not rely on the change in luminance that would accompany the approach of a dark object, so that reversing the contrast of the approaching object does not reverse the directional selectivity of the LGMD 1 and 2 neurones. The two critical image cues are extracted locally without reference to global image patterns so their computation is very fast. The use of two cues adds robustness to the LGMD 1 and 2 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 maxi-
mised. These cues embody the rate of expansion of an object’s retinal image.

The two LGMD neurones do not share exactly the same input organisation, as can be seen by their responses to the cross-hairs stimuli shown in Figure 5. Unlike the LGMD 1, the LGMD 2 receives no excitation from afferents excited by increases in illumination so it is not excited by light approaching objects (Rind, 1987; Simmons and Rind, 1997).

**Tuning for a Collision Trajectory and Responses to Object Approach Against a Moving Background**

The tuning of the LGMD 1 and 2 for a collision trajectory is tight. When measured as total spike numbers, the tuning curve has a half width at half height of 3.0°, a value similar to collision sensitive neurones in the nucleus rotundus in the pigeon (3.3°, Sun and Frost, 1998; Wang and Frost, 1992). The tuning is dependent on the exact feature of the DCMD response measured; if instead of total spike number, the peak spike rate is used, the tuning observed is even tighter with a half width at half height of 1.8°. The locust may use more than one aspect of the DCMD response to guide its behaviour making it important to consider a variety of tuning indicators (Childs, 2000; Judge and Rind, 1997). The evidence presented so far points to a role for these neurones as collision detectors but what of their responses in a more natural visual context? We have examined the response of the LGMD 1, 2, and DCMD to single approaching objects with no other image motion. When the locust moves on the ground or in the air, an object will approach against a background of self-generated image motion. The response of the LGMD 1, 2, and the DCMD to an approaching object is reduced when the approach occurs against a moving background, consisting of a drifting sinewave grating (Rind and Simmons, 1992; Simmons and Rind, 1997). The reduction in response was greatest for velocities of 100–800°/s, and spatial frequencies of 10–20° (Fig. 6) but the response was never completely eliminated. In particular, the timing of the peak spike rate was resistant to the presence of drifting wide-field gratings. The IPSP at the termination of object approach is clearly visible (Fig. 6C) in the intracellular records made from the LGMD 2 in the presence of drifting wide-field grat-
ings of different spatial and temporal frequencies (Rind and Simmons, 1992; Simmons and Rind, 1997).

INPUT ORGANISATION OF THE LGMD CONTRIBUTING TO ITS DIRECTIONAL RESPONSES: MODELLING AND ROBOTIC STUDIES

As noted previously, the selectivity for approach is achieved by responding to the increasing extent, and velocity, of image edges moving over the retina (Simmons and Rind, 1992, 1997). Although the synaptic inputs to the LGMD I had been known for some time, they were not initially understood in terms of the selectivity of the LGMD/DCMD neurons for rapidly approaching objects. When such features were incorporated into a biological neural network, it also responds selectively to objects approaching on a collision course (Rind and Bramwell, 1996).

Modelling Studies: The Network and Its Inputs.

The network incorporated the general features of a locust eye, including the input organisation of the LGMD and DCMD neurons described above (Rind and Bramwell, 1996; Rowell et al., 1977). The excitation in the P-unit was 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 (James and Osorio, 1996).

The excitation from the P-units was 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 were summed by “S”-units in layer-3, which excited the “LGMD” in layer-4. Synaptic and conduction delays within and between layers could be set independently. However, for the simulations described here, delays at excitatory connections between layers were set to zero ms, whereas delays on inhibitory connections varied between 1–4 ms. Setting delays greater than zero at the excitatory connections only served to shift the whole response to the right along the time axis. Excitation of a layer-2 E-unit followed activation of the P-unit feeding it, unless the unit was within its refractory period. Excitation in the E-unit, like the other retinotopic units, followed a fixed time course with a peak followed by an exponential decline. The time course of the decline was set by the time constant for the type of unit with decay at inhibitory units being

Fig. 7. Schematic representation of the neural network LGMD pathway to show the parallels with the locust LGMD pathway. The input organisation of the basic retinotopic unit of the network is labelled. The output activity of 250 of these units converge on the LGMD unit. In each layer, proximity to the central retinotopic unit is indicated by the shade of grey. The time course of activation, of each different P, I, E, and S unit, is shown at the bottom, normalised to a 0–1 scale. This time course of activation in I, E, and S units represents the time constant of the decay in activity following a stimulus exceeding a threshold value. 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). (Modified after Rind and Bramwell, 1996.)
slower than at excitatory ones. (lower graphs Fig. 7, T.)
12.3 ms E-unit; 55 ms, I-unit; and 22.2 ms, S-unit.
This envelope of excitation in each unit corresponded to
summed epsps and spikes. In layer-2, each E-unit
passed excitation to one layer-3, S-unit in the same
retinotopic position, and each I-unit passed inhibition
laterally to two rings of S-units, centred on the I-unit.
The inhibition passed from the I-unit to each nearest
and next-nearest S-unit was always divided by the
number of such connections made by the I-unit. Thus,
1/6 of the input excitation was passed to each nearest,
and 1/12 to each next-nearest S-unit. This inhibition
passed on by an I-unit to each nearest and next-nearest
S-unit could then be further altered by changing the
synaptic weighting of the I-unit input. This synaptic
weighting was expressed as the percentage of I-unit
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synaptic weighting of the I-unit input. This synaptic
S-unit could then be further altered by changing the
passed on by an I-unit to each nearest and next-nearest
S-unit. This inhibition to the nearest and to the next-nearest layer-3
S-units was also delayed by a selected amount, relative to
the excitatory input. This resulted in a balance be-
tween excitation passing from layer to layer down the
network and inhibition directed laterally.

The E and I inputs were summed linearly by each
S-unit in layer-3 until a given threshold level of exci-
tation was reached and a spike was produced (Fig. 7,
bottom panels). After the peak of a spike, voltage de-
clined exponentially with time and was followed by a
refractory period. This phase of the S-unit response
was independent of any inhibitory input. Buildup of
excitation in an S-unit was not shown, only its supra-
threshold output. Layer-4 of the model consisted of a
single LGMD-unit, which linearly summed excitation
from all active S-units and inhibition, delayed by
2–5 ms, from the inhibitory F-unit. This sum was ex-
pressed 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 constituted a
feed-forward pathway, bypassing layer-3, and was only
active when a set number of P-units (about 50) were
activated in a short time. For each simulation, the
threshold number of photoreceptors excited before ac-
tivation of the loop occurred and the activity in the
feed-forward inhibitory F-unit could be set. The initial
increase in activity and then the rate of decay were
both controlled by the rate of P-unit activation or inac-
tivation. Following activation, of an E-, I-, or S-unit,
extcitation in it declines exponentially (Fig. 7, bottom
panels).

Network: Monitoring Network Activity During
Each Simulation. Activity in the LGMD, the output
element in layer-4 of the network, was displayed at the
end of each simulation as a graph of excitation, on a
scale of 0–400, against time (Fig. 8A and B). During
each simulation, a graphic display was 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 output element of
the neural network, the LGMD, responded direction-
ally when challenged with approaching vs. receding
objects, preferring approaching objects (Fig. 8). Direc-
tional selectivity was maintained with objects of various ap-
proach velocities. Directional selectivity for rapidly ap-
proaching objects was 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 were excited in a short time. The inhib-
itory loop was activated at the end of object approach,
truncating the excitatory LGMD response after ap-
proach has ceased, but at the initiation of object reces-
sion (asterisk in Fig. 8A and B). The model predicted
that there would be strong activation of the feed-forward
pathway onto the locust LGMD 1 at the end of
object approach and also during object recession.
Intra-
cellular recordings from the LGMD 1 and 2 neurones
revealed clear evidence of IPSPs at the time predicted
by the model (see Figs. 4 and 6C; Rind and Bramwell,
1996; Rind, 1996; Simmons and Rind, 1998).
The model also revealed the importance of the critical race between excitation generated by the moving edge of the object and the inhibition extending laterally within the network. Excitation tracks the moving and growing boundary edge of the image, whereas the inhibition spreading laterally from the same edge moves with a delay. When the image edge moves fast enough, the excitation it generates escapes the inhibitory influence of the lateral inhibition and the response in the network builds up very rapidly. An object approaching on a collision trajectory has maximal edge expansion and an exponential increase in the velocity of edge motion, ensuring that excitation wins the race with the laterally directed inhibition. When the lateral inhibition is unable to win this race, or it is removed from the network, the directional response of the LGMD is reduced (Rind and Bramwell, 1996). The critical race probably occurs over the surface of the LGMD 1 or 2 dendrites in the lobula, as the synaptic input arrangement is consistent with this (Rind and Leitinger, 2000; Rind and Simmons, 1998). Tonic lateral inhibitory networks at the level of the lamina monopolar neurones may also be important in this regard (Blanchard, 1998).

**Incorporation of the LGMD Network in the Control Structure of a Small Mobile Robot**

In a recent series of experiments (Blanchard et al., 2000), a software package, IQ-R-4-21, developed by Mark Blanchard and Paul Vershure at the Institute for Neuroinformatics, Zürich, was used to encode the LGMD network, described above, into the control structure of a small mobile Khepera robot, and to track the motion of the robot in a test arena (see Figs. 9,10). A graphics interface enabled the activity in all the layers of the input organisation of the network to be monitored during the robot’s movements so we could follow the responses to particular image features in a scene.

The results of these tests were promising both in terms of the behaviour of the robot and the use of the simulation software. The robot avoided collisions 91% of the time at speeds of 2.5 cm/s; 81% at speeds of 5 cm/s and 88% at speeds of 10 cm/s (see Fig. 10). The effectiveness of control via the LGMD was significantly better than 50% at every speed tested (1.5–12.5 cm/s). At the highest translation speeds, the robot crossed its environment in approximately 3 seconds so the time between an avoidance reaction and the robots next encounter with an obstacle could be short. Testing the ability of the model to signal the approach of real, rather than idealised visual stimuli, was also an important stage in developing the model for real-world applications. The locust LGMD neurone provides information to improve the performance of the artificial system and the artificial system allows us to understand the constraints of the LGMD in a real world situation in a way that would be impossible in a living locust.

**Visual Neurones Responding Selectively to One Direction of Motion at a Fixed Distance from the Locust**

Visual neurones in this second category respond selectively to a particular pattern of image motion over a substantial part of the eye, generated by the locust’s own movements through its environment. These motion detectors underlie the locust’s optomotor responses that result in the stabilisation of the insect’s flight speed and heading direction, through the perception of self-generated image flow fields. The motion detecting neurones underlying these reactions show directional responses and are best tuned to deviations...
about one of the three principal body axes (see Fig. 2). In the locust optic lobe, the visual neurones on this pathway are much less prominent than comparable neurones in the fly, and are smaller in size than the locust’s collision sensitive neurones (Franceschini et al., 1992; Rind, 1984, 1990a,b). Direction selective motion detectors of this type (Fig. 11A,B) have been recorded in the locust optic lobe as far peripherally as the medulla (Osorio, 1986). In these medullary neurones, directional selectivity arises as an inhibitory interaction between two flicker sensitive inputs (Fig. 11C) and the inhibition is strongest at separations of 2–3°. The neurones fall into a single anatomical class (Fig. 11A) and are excited by upwards motion over their receptive field (Fig. 11B). Their receptive fields are directed ventrally looking downwards and extending 20°, over several retinotopic units (Osorio, 1986). The neurones can detect image drift velocities ranging from below 0.02°/s to above 200°/s. This lower velocity corresponds to the stimulus traversing the receptive field of one photoreceptor in about a minute (Osorio, 1986). The neurones bypass the lobula so would not provide inputs for the directionally selective neurones found there (Rind, 1990a,b).

Wide-field directionally selective motion detecting (DSMD) neurones with preferred directions of motion either forward (Fig. 12A–C; DSMD (F)) or backward (Fig. 12D–F; DSMD (B)) over the eye have been described in the locust lobula (Rind, 1990a,b). The neurones receive excitatory postsynaptic potentials in response to motion over the eye in one direction and inhibitory postsynaptic potentials in response to the opposite (Fig. 12B,C). The DSMD neurones project into the protocerebral region of the brain (Fig. 12A,D) where they are known to make excitatory connections with a descending neurone integrating motion over the two eyes (Fig. 12E,F). The descending neurone is excited by backward motion over the ipsilateral eye and forward over the contralateral (Fig. 12E; and downward stepping in stimulus trace in Fig. 13i–iv) creating a neurone maximally excited by yawing motion of the locust about its vertical axis (Fig. 2). The elementary motion detectors providing input to the locust descending DSMD neurones are of the correlation variety, as the curves of neuronal activity vs. temporal and spatial frequency show clear optima at spatial frequencies of 0.035 cycles/degree (29° in λ) and at temporal frequencies of 15.6 Hz with a steep roll off above 22 Hz (Rind, 1990a). Such directionally selective descending neu-
Fig. 12. Characterisation of directionally selective motion detectors from the locust lobula and their connections with descending neurones. A: Morphology of a stained directionally selective motion detector with a preferred direction forwards over the ipsilateral eye, LDSMD(F). The neurone has been drawn from a whole mount of the brain drawn from behind, the large trachea entering the brain serves as a landmark. The extent of the lobula is shown by a dotted line. B: LDSMD(F) neurone receives excitatory postsynaptic potentials (PSPs) in response to forward phi (apparent) motion produced by illumination of neighbouring LEDs in a nine LED arc, over the ipsilateral eye (top pair of traces) and, inhibitory PSPs in response to backward motion. Each Phi motion is indicated by a step in the bottom trace of the pair, a downward steep indicates forward motion and an upward step indicates backward motion. There was no input in response to phi motion over the contralateral eye (not shown). To reveal the underlying PSPs, the neurone has had spikes blocked by intracellular injection of hexammine cobaltic chloride. C: Intracellularly recorded response of a LDSMD(F) neurone to two velocities of motion generated as in B. In the absence of motion, the neurone produces spikes. Motion in the preferred direction, forward over the ipsilateral eye, increases the number of spikes produced, and motion in the non-preferred direction reduces it with clear IPSPs visible. A downward steep on the stimulus monitor indicates forward motion. D: The output morphology of a LDSMD with a preference for motion backward over the eye LDSMD(B). The dotted line indicated the border of the dendritic arborisation. The neurone made an excitatory, monosynaptic connection with a descending neurone with a cell body and dendrites in the ipsilateral protocerebrum. E,F: Intracellular recordings from the two synaptically linked directionally selective neurones shown in D above. E: At low spike rates, a single spike in the LDSMD(B) neurone (top) leads to an EPSP in the PDSMD neurone (bottom). Two spikes in the LDSMD(B) neurone in quick succession are needed for a spike in the post synaptic neurone. F: Signal averaged response (eight sweeps). The LDSMD(B) spike (top) and the induced EPSP (bottom) are shown on an expanded time base. The EPSP follows a spike in the LDSMD(B) with a 2-ms latency. B: Top trace, scale bar = 20 mV; bottom vertical scale bar = 50 mV. C,E,F: Scale bars = 5 mV. (Modified after Rind, 1990a.)
rones provide the locust with a sensitivity to deviations around all three axes, yaw, pitch, and roll, as well as a sensitivity to the flow field created by straight forward flight (Baader et al., 1992; Kien, 1974; Reichert et al., 1985; Rind, 1990a,b).

**Ecology of Wide-Field Motion Detectors**

A recent study relating motion detector tuning to the visual ecology of 10 insect species examined the hypothesis that the visual ecology of an animal may be reflected in the tuning of its motion detectors (O'Carroll et al., 1996). The optimal tuning curve of a motion detector should tell us something about the types of motion the detectors are good at dealing with. For example, neurons of fast flying insects such as bumble bees and butterflies (Table 1) are tuned to higher frequencies than those of slower flying insects or ones that hover, such as bee-flies and hawkmoths. Motion detectors in the locust nerve cord (Fig. 14), like those of the fast flying bumble bee, are tuned to high-image velocities (Rind, 1990a).

**CONCLUSIONS**

Invertebrates and locusts in particular reveal a range of visual behaviours controlled by a tractable amount of neural machinery: a locust brain is about 3 mm from retina to retina and weighs 0.004 g. The locust possesses a sophisticated and rapid image processing system that is providing an understanding of the neuronal interactions that create a selective tuning to looming objects that are approaching on a collision trajectory. Locust collision sensing neurones have been successfully incorporated into the control structure of a mobile robot and the system performs robustly in a world more complex than that normally used to challenge the locust LGMD 1 or LGMD 2 neurones.

In addition, directionally selective motion detectors in the optic lobe signal motion of the locust relative to its surroundings. These wide-field neurones in the lobula project into the protocerebrum where they synapse with descending interneurons that combine inputs from the two eyes or of several modalities. Thus, the output of these motion detectors can be used to signal forward flight speed or to correct unintentional deviations from a straight flight path.

**TABLE 1. Comparison of the tuning of motion detectors from a variety of animal species (from Rind, 1990a; O'Carroll et al., 1996)**

<table>
<thead>
<tr>
<th>Animal</th>
<th>Spatial frequency optimum (cycles°)</th>
<th>Temporal frequency optimum (cycles/sec)</th>
<th>Velocity (°/sec)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Locust</td>
<td>0.035</td>
<td>16</td>
<td>457</td>
</tr>
<tr>
<td>Bumble bee</td>
<td>0.05</td>
<td>25</td>
<td>500</td>
</tr>
<tr>
<td>Hawkmoth</td>
<td>0.05</td>
<td>2.0 diurnal</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.7 nocturnal</td>
<td></td>
</tr>
<tr>
<td>Hoverfly</td>
<td>0.105</td>
<td>5</td>
<td>48</td>
</tr>
<tr>
<td>Human</td>
<td>2.0</td>
<td>4</td>
<td>2</td>
</tr>
</tbody>
</table>

*A moving sinewave grating was used to estimate the spatial (cycles°) and temporal frequencies (cycles/sec) leading to an optimal response from each motion detector. These values can also be used to give the optimal velocity tuning (°/sec) of the motion detectors.*
REFERENCES


