

Review article

Possible functions of a population of descending neurons in the honeybee's visuo-motor pathway

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Summary — An identified population of honeybee descending neurons (DNs) responds to wide-field motion over the compound eyes. They give non-habituating, directionally selective responses which adapt to continued motion. Contrast sensitivity functions show the responses depend on luminance, contrast, spatial and temporal frequency. The distribution of the DN's outputs in the thoracic ganglia is consistent with changes in muscular activity required for particular compensatory movements. These features suggest the DN's lie along the optomotor pathway. The DN's responses have different time-courses. This might reflect distinctions in their putative inputs and between pathways implicated in different aspects of visually mediated flight control. The responses of horizontal DN's to contraction and expansion and to unidirectional motion were compared revealing differences in the way they integrate the monocular components of binocular flow-fields and how velocity and spatial structure effects this integration. It is possible the DN's are convergence site(s) for substrates underlying different behaviours each triggered by specific optical flow templates.

descending neuron / vision / motion sensitivity / directional selectivity

INTRODUCTION

The honeybee's ability to discriminate between colours (von Frisch, 1914; Menzel, 1967) and shapes (Anderson, 1972) and perceive depth (Srinivasan *et al*, 1989) and distance (Kirchner and Srinivasan, 1989; Srinivasan *et al*, 1991) is impressive. Contemporary analysis of the honey-

bee's extensive list of visually mediated free-flight behaviours is making us increasingly aware of the sophistication of the underlying visual system. Like most diurnal flying insects the honeybee's natural visual environment is an opulent assortment of optical information. The large visual field of her compound eyes is filled with an array of spectral wavelengths and

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luminance modulations, all distributed non-uniformly and moving over her eyes in different directions relative to her body as she flies. From this veritable cacophony of visual information the honeybee is able to extract and process that information which is relevant to the control of her flight course and speed, both rapidly and accurately. There is currently much interest in the mechanisms which underlie the extraction of different types of visual information in the insect visual pathway. In this paper we consider a population of neurons involved in the process in the honeybee and examine the way in which certain sorts of information are simplified before being transmitted to the motor centres.

Wehner (1987) pointed out that information is filtered by insects at the most peripheral level in a way that is matched to the solution of a particular task. Behavioural evidence suggests that the honeybee's visual system simplifies its task by separating colour from motion information (*eg* Lehrer *et al*, 1990). Certainly many motion-sensitive behaviours in the bee such as optomotor responses (Kaiser and Liske, 1974; Kaiser, 1975); movement-avoidance responses (Srinivasan and Lehrer, 1984) and aspects of tracking moving targets (Zhang *et al*, 1990) are chromatically independent. This duality in the honeybee has been compared with the situation in vertebrates (*eg* Zhang *et al*, 1990; Lehrer, 1991) where perception of motion is believed to be subserved by the colour-blind magnocellular pathway (Livingston and Hubel, 1987). Recent neuro-anatomical studies by Strausfeld and Lee (1991) support the presence of 2 parallel retinotopic pathways in the insect optic lobe which appear to arise from each ommatidium within the retina. These authors suggest that this could form the basis of 2 independent pathways for colour and for motion in insects. The task of the pathway which concerns us in this article is that of

guiding and stabilising the honeybee's flight upon the basis of motion information.

We have physiologically characterised a large number of identified interneurons which descend from the brain to the thoracic motor centres of the bee (Fletcher *et al*, 1984; Goodman *et al*, 1987, 1990, 1991; Ibbotson, 1990, 1991; Ibbotson and Goodman, 1990; Bidwell, 1992). Analysis of the response characteristics of these descending neurons (DNs) shows that they give directionally selective responses to widefield motion over the compound eyes and suggests that they might represent one of the final stages of a motion processing pathway. They thus provide a tool with which to examine the way the different parameters that influence motion processing have been filtered and matched to the requirements of flight control.

The response properties of the neurons were examined by stimulating the bee using either mechanically moved square-wave gratings or electronically generated sine-wave gratings ("Constable" image generator, Cardiff Visual Systems) presented on an X-Y display monitor (Tectronix 608). Specific details of the stimulating regimes for each experiment are included in the legends of appropriate figures. Following intracellular recordings the cells were identified by iontophoretic injection of dye, either cobalt chloride (Goodman *et al*, 1990, 1991; Ibbotson and Goodman, 1990; Ibbotson, 1991; or Lucifer yellow (Bidwell, 1992).

THE DIRECTIONAL SELECTIVITY OF THE DNs

The response of the bee DNs is maximal for motion in one direction, the preferred direction (*eg* figs 2a, 3a, 4a). Like the responses of directionally selective (DS) cells throughout the insect visuo-motor

pathway (eg fly lobula plate neurons: Hausen, 1984; motor neurons: Milde and Strausfeld, 1990) the response of the DNs gradually declines as the direction of motion subtends a larger angle with the preferred direction. The peak responses of the DNs tend to occur for motion along the vertical or the horizontal and their preferred directions can be broadly defined as: progressive, regressive, upwards or downwards motion (eg, figs 1a-d). This physiological division into vertically or horizontally tuned cells can be correlated with certain anatomical characteristics of the cells within the brain, morphologically distinct DNs being grouped together on the

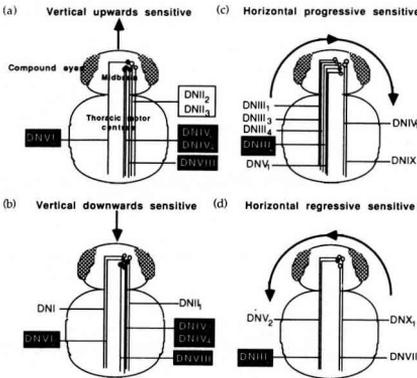


Fig 1. A diagrammatic representation of the neurons maximally excited by (a) upwards; (b) downwards; (c) progressive; and (d) regressive wide-field motion. The honeybee is viewed from above. The somata of neurons which respond exclusively to one direction of motion over the frontal or lateral regions of the eyes are represented by empty circles. The somata of neurons which respond to more than one direction of motion over the frontal or lateral regions of the eyes are shown by filled circles and shaded annotations. Only one cell of each pair of descending neurons is shown. Some of the neurons descend to the thorax on the same side of the body as the side in which the soma lies (ie ipsilaterally; eg DNI₂ - a). Other neurons descend to the thorax on the opposite side to the side of the body in which the soma lies (ie contralaterally; eg DNI₁ - c).

basis of the location of their dendritic fields in the midbrain neuropile (eg Ibbotson, 1990). Two discrete populations of DNs (DN clusters) have been identified. The pri-

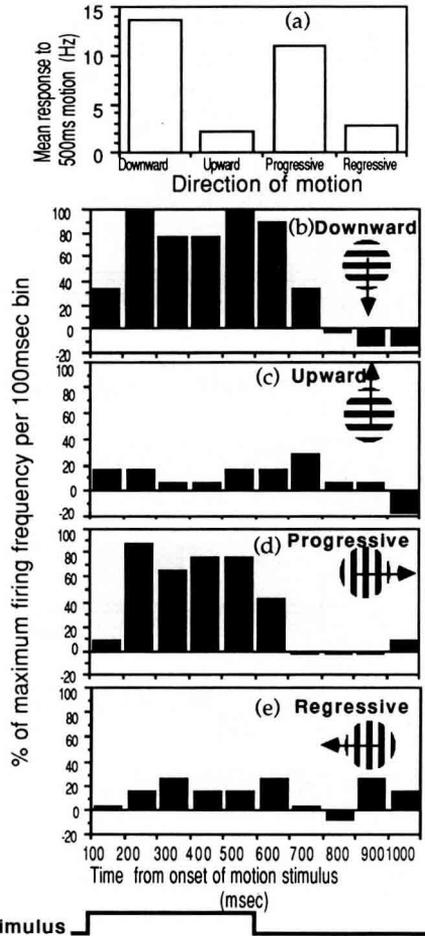


Fig 2. The motion induced response of DNI₁. Since-wave gratings were moved in each of 4 directions: downwards, upwards, progressive and regressive for 500 ms over the frontal regions of the eyes. Over 500 ms stimulation the grating elicits the highest rate of firing relative to baseline frequency when it moves downwards (a). When spikes were counted in 100 ms bins from the onset of stimulation the maximum spike frequency per 100 ms bin occurs 100-200 ms after the onset of stimulus (b-e).

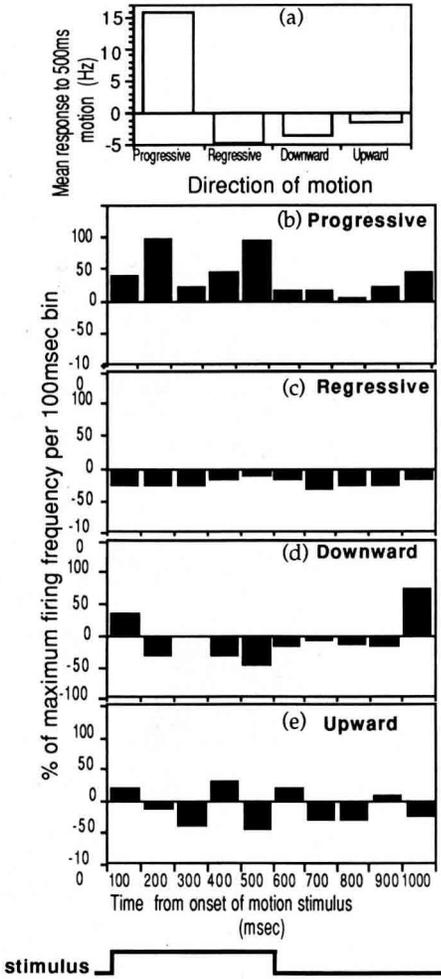


Fig 3. The motion-induced response of DNIII₃. Since-wave gratings were moved in each of 4 directions as described for figure 2. Over 500 ms the grating elicits the highest rate of firing relative to baseline frequency when it moves progressively (a). The maximum spike frequency per 100 msec bin for DNIII₃ occurs 100–200 ms after the onset of the stimulus (b–e). Mean values were calculated from the response of 2 cells.

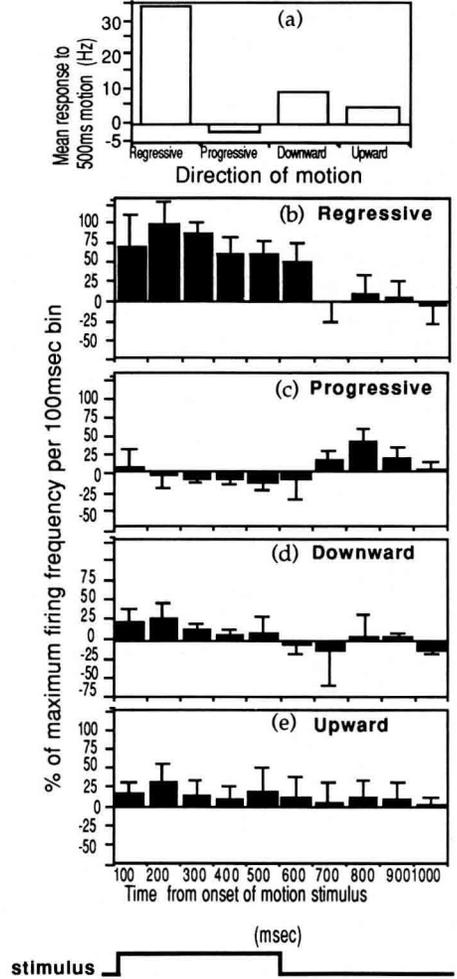


Fig 4. The motion-induced response of DNVII. Sine-wave gratings were moved in each of 4 directions as described for figure 2. Over 500 ms the grating elicits the highest rate of firing relative to baseline frequency when it moves regressively (a). The maximum spike frequency per 100 ms bin for DNVII occurs 100–200 ms after the onset of the stimulus (b–e). Error bars show the SD for 4 DNVII cells.

mary dendritic fields of DNs in the first cluster are located in the postero-lateral deuto-tritocerebrum and overlap with the terminals of lobula neurons which have travelled in posterior optic tract I (POT I). In the second cluster the dendritic arborisations of the DNs are restricted to the postero-dorsal deutocerebrum in the vicinity of the axon terminals of lobula neurons in posterior optic tract II (POT II). In the fly separate mid-brain projection centres have been shown to be associated with the terminals of either horizontally or vertically sensitive lobula neurons (Hengstenberg *et al*, 1982). The terminals of vertically sensitive lobula neurons connect with the dendrites of a cluster of vertically tuned descending cells and the horizontally sensitive lobula neurons are associated with the dendritic branches of horizontally-tuned descending neurons (Eckert, 1981; Strausfeld, 1984; Strausfeld *et al*, 1987). An analogous segregation of directional selectivity appears to exist in the honeybee as DNs within each cluster associated with POT I or POT II share a common preference for either horizontal or vertical motion (Ibbotson, 1990). This division corresponds with that proposed for lobula neurons which travel along POT I (Hertel and Maronde, 1987) and POT II (Ibbotson, 1990) respectively.

The convergence of directionally specific motion information at targets in the brain may have 2 potential functions, both of which are of interest in the context of operations at the lobula-DN interface. One function of directionally-specific targets in the brain might be to maintain vertical and horizontal selectivity. Thus targets simply act as a funnel into the DNs for information of the same directional persuasion. Ibbotson (1989) identified 2 morphological features which distinguish the vertically tuned from the horizontally tuned DNs. A faster visuo-motor connection is inferred by the larger axonal diameter, 10–15 μm , of verti-

cally sensitive DNs. Ibbotson also proposed a more direct visuo-motor connection based on the location and structure of the terminal branches of vertically sensitive DNs in the thoracic motor centres. The vertical DNs have short, stubby branches in the latero-dorsal neurophile which might provide a direct synaptic contact with the dendritic trunks of direct flight motor neurons. The more ventrally located thin, beaded terminal fibres of the horizontal DNs spread diffusely throughout the ganglia. This suggests that horizontal DNs connect to the dendritic branches of interneurons of the premotor circuitry, which might correspond to a less direct route with an extra level of processing. Parallel flow of vertical and horizontal information to the DNs permits the distinction between direct and indirect transfer from them. This distinction might be adapted to suit the requirement of the motor output. For example, fewer synaptic stages in the vertical network would reduce transmission time for input used to stabilise flight. Concomitantly, more processing stages in the horizontal network might refine the accuracy of signals used in the precise control of flight direction and speed.

A second potential function for vertical and horizontal parallel flow is the possibility of flexible integration of sensory data. This might include incorporating the outputs of both the vertical and horizontal systems to enhance the specificity of the responses of some DNs. The specificity of the DNs directionally selective responses is wide ranging. Take for example the specificity of the responses of 2 DNs sensitive to vertical motion (see fig 1b). The firing frequency of DNI in response to downwards motion is 10-fold higher than its firing frequency in response to horizontal motion. Less specific is the response of another vertical cell, DNII₁, which responds only slightly more (1.2-fold) to downwards motion than horizontal motion. A correla-

tion between the relative size of the DNs' responses to vertical and horizontal information and the period of time taken for them to achieve their maximum rate of firing suggests that those cells which convey more directionally specific information require a longer time to arrive at their maximum response level (fig 2b). By counting spikes in 100 ms bins from the onset of the movement stimulus, a crude estimate of the time taken to reach maximum firing frequency was extrapolated. Of the 2 vertically tuned cells mentioned above, DNI takes 248 ms to reach 75% of its maximum firing frequency whilst DNII₁ takes only 138 ms to reach 75% of its maximum firing frequency. The correlation also holds true for the horizontally sensitive cells. For instance, the time required to reach 75% of the maximum rate of firing by 2 regressive sensitive cells, DNVII and DNIII₃ is 137 ms and 167 ms respectively. DNVII responds to horizontal motion twice as much as it does to vertical motion, whilst DNIII responds with excitation to progressive motion only. The various degrees of directional specificity suggest that a precise signal obtained by 'filtering' is not a functional prerequisite for motor output and in certain circumstances would perhaps be a disadvantage. Specificity in the DNs seems to demand time and it may be that for some signals accuracy is accomplished at a later stage (*eg* at the thoracic motor centre).

HOW IS THE INFORMATION SIGNALLED BY THE DNs RELATED TO THE LUMINANCE CONTRAST OF THE BEES SURROUNDINGS?

The visual system maintains invariance in conditions of varying illumination by responding to contrast. Surfaces absorb or reflect a constant fraction of incident light, so that the relative intensities of objects

are constant, provided they are uniformly illuminated. The response (firing frequency) of the DNs increases with the luminance contrast of a moving sine-wave grat-

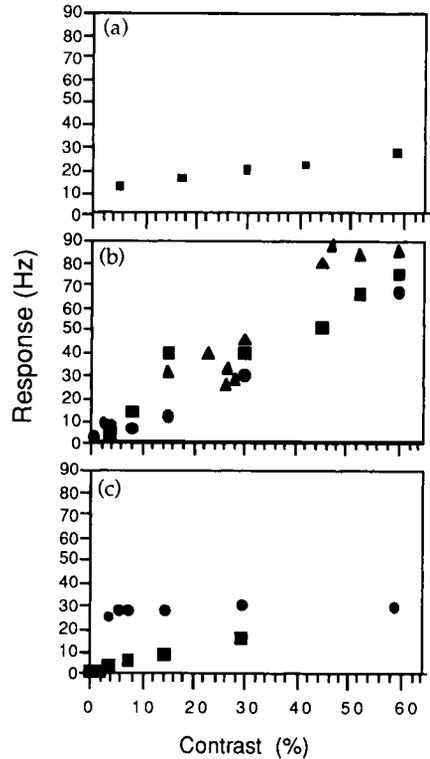


Fig 5. Contrast response functions for the DNs. **(a)** The averaged response of 20 DNs to gratings moving in each cell's preferred direction over the lateral regions of the field. The mean luminance of the grating was 0.02 cd/M² and its drift generated a temporal frequency of 11 Hz. **(b)** The response of DNIII1 (filled squares); DNI (filled circles) and unidentified vertical cell (filled triangles) to motion in their preferred directions over the frontal regions of the field. The mean luminance of the grating was 2.0 cd/M² and its drift generated a temporal frequency of 11 Hz. **(c)** The response of DNIII₂ to motion in its preferred direction (upward: circles) and non-preferred direction (progressive: squares) over the frontal regions of the compound eyes. The mean luminance of the grating was 2.0 cd/M² and its drift generated a temporal frequency of 11 Hz.

ing (fig 5a–c). The absolute responses in some of the DNs increases approximately in proportion to ΔI^2 (fig 5a, 5b) but this is not true for all of them. The shape of the contrast–response function (firing frequency *versus* contrast) in the DNs depends upon background luminance. When adapted to lower luminances the contrast response approximates to a straight line with a shallow slope (fig 5a), but when adapted to higher luminance the contrast–response function becomes steeper (fig 5b).

The luminance contrast which gives visual texture to the panorama has a wide range. However, the range of contrasts produced by objects in habitats uncontaminated by human artefacts is relatively small. By sampling points in a number of images, using a scanner with the same angular and spectral sensitivity as a fly's eye, Laughlin (1981) found that their average contrast was 40%, with the majority of contrasts < 50%. The visual system exploits the information most commonly encountered in scenes, at least in the natural environment. Thus the most efficient operation of the motion detection system has evolved by devoting its dynamic range to the lower end of the distribution of contrasts in natural scenes at the expense of coding the rare high contrasts which are associated with specular reflections and light sources. Like the contrast–response curve of lamina monopolar cells (LMCs) in the fly (Laughlin *et al.*, 1987) the contrast–response curve of the majority of the DNs is non-linear with a characteristic sigmoidal shape. The dynamic range of the DNs in the bee also resembles those of other neurons higher in the visual pathway, such as H1 in the fly lobula (Dubs, 1982), from which one can infer that the exploitation of the statistical distributions of contrast in natural scenes is an ubiquitous tool in insect motion pathways.

Interneurons such as the DNs and the behavioural responses they drive are high-

ly sensitive to moving gratings composed of very low contrast ($\Delta I/\text{mean } I$) elements. For moving gratings at contrast values < 3–4% the walking responses of *Drosophila* (Heisenberg and Buchner, 1977) and flight responses of *Musca* (McCann and MacGinitie, 1965) approximate to a parabola which indicates a dependence on ΔI^2 . The exquisite sensitivity to small fluctuations of low contrasts of both motion-induced behaviour and the bee DNs exemplifies the conservation of the initial signal at all levels of the pathway.

WHAT RANGE OF SPATIAL FREQUENCIES ARE USED TO SIGNAL MOVEMENT OF THE HONEYBEE'S SURROUNDINGS?

To provide a robust neural representation of the retinal stimulus, only those signals that provide a high signal:noise ratio and represent rich motion cues are transmitted. Filtering, either peripherally or as a consequence of the motion detecting process, thus determines the information that is used to control motion-induced behaviour. Sine-wave gratings are used to examine the spatial frequency response of the visual system or some part of it in terms of the spatial contrast sensitivity function (CSF). The CSF can reveal which spatial frequencies, if any, are filtered from optical signals, and has been used to infer the processing level at which filtering might occur (*eg* Srinivasan and Dvorak, 1980). Contrast sensitivity is measured by determining the minimum amount of contrast (threshold contrast) required of a grating to evoke a significant motion response. Contrast sensitivity is the reciprocal of threshold contrast and varies with sinusoidal spatial frequency. The CSFs shown here were established by locating the contrast of a grating of defined spatial frequency where a DN displayed significant directional selectivity by differentiat-

ing between null and preferred motion using a modified binary bracketing routine (Tyrell and Owens, 1988).

All the CSFs established for the bee DNs at higher luminance peak in the range 0.03–0.06 cpd when the temporal frequency generated by the moving grating was 11 Hz (fig 6a). At lower luminances, over the lateral regions of the visual field, the

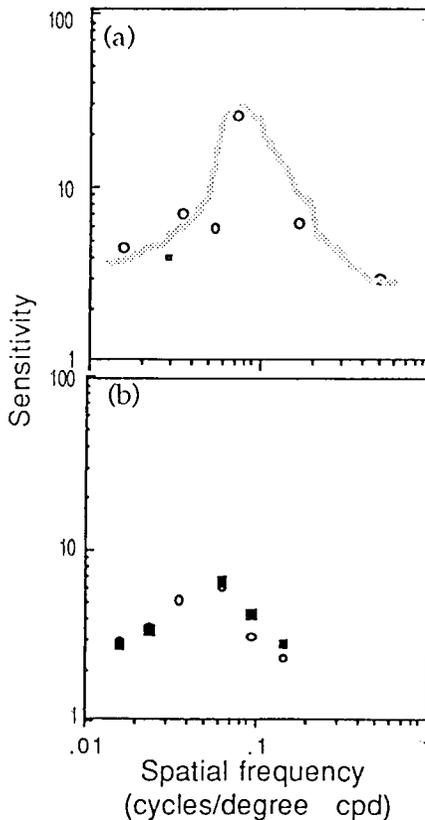


Fig 6. Contrast sensitivity functions for (a) DNI_2 to gratings of mean luminance 2.0 cd/M^2 moving over the frontal regions of the field and (b) for cells sensitive to progressive (filled squares) and regressive (open circles) to gratings of mean luminance 0.2 cd/M^2 moving over the lateral regions of the field. The spatial frequency of the moving grating was measured in cycles/degree of visual angle (cpd).

sensitivity peak shifts towards lower values of spatial frequency as shown for 2 horizontally sensitive cells (fig 6b). The DN's contrast sensitivity as a function of spatial frequency is approximately within the same range as cells higher in the insect visual pathway such as medulla cells terminating in the midbrain of the butterfly, *Papilio* (Maddess *et al*, 1991) and the lobula plate giant cells terminating in the mid-brain of the flies *Musca* and *Lucilia* (Dvorak *et al*, 1980; Srinivasan and Dvorak, 1980). The spatial frequency specificity of the DNs compares better with that reported for the medulla cells of *Papilio* than with those reported for the lobula plate cells of the fly or the lobula cells of the locust (Rind, 1990).

The DNs share the characteristic low spatial frequency attenuation of DS cells found in the lamina of the fly (Dubs, 1982) the medulla of the butterfly *Papilio* (Maddess *et al*, 1991) and also in more divergent species such as *Limulus* (Brodie *et al*, 1978) and in humans (eg Kelly, 1979). For a motion detecting system low spatial frequency attenuation is advantageous because it blocks the dc or zero-movement cues. These are readily transmitted by the optics of the compound eye and produce greater Fourier power but are of limited use in detecting the displacements likely to occur during flight (Dvorak *et al*, 1980). At high levels of luminance the movements of flies, for example, seldom displace the visual scene by $> 10^\circ$ (Reichardt and Poggio, 1976). By calculating the signal spectra generated by a moving random pattern, Srinivasan and Dvorak (1980) found that for the normal displacement expected of a fly the optimal spatial frequency would be between 0.05–0.1 cpd. Thus the low spatial frequency roll-off shown by the insect motion pathway suggests that the mechanisms which filter and process signals optimise the spatial frequency range for the most usual displacements made.

One explanation that can be offered for the different spatial frequency sensitivities of the DS cells of the medulla, lobula and ventral nerve cord might be that they are due to interspecific differences. This would simply imply that the peripheral filtering along the pathways of the honeybee and the butterfly removes much more of the low spatial frequency information than filtering along the pathway of the fly and the locust. If species differences are ignored it might be conjectured that more than one motion pathway conveys information through the optic lobes to the central brain. These parallel pathways display different filtering properties: one does not remove low spatial frequencies, as illustrated by the CSF of lobula plate giant cells, the other pathway includes stronger lateral inhibitory interactions producing the low spatial frequency roll-off of the CSF displayed by medulla cells. The DNs might then receive inputs from the pathway with the tighter lateral inhibition, perhaps from analogues of the medulla cells in *Papilio*.

The sensitivity of the DNs to gratings of different spatial frequencies was examined at different drift velocities. The DNs are most sensitive to movement when it generates a temporal frequency (or contrast frequency, CF) of 8–11 Hz (Ibbotson and Goodman, 1990; see also figs 7–8). Maximum contrast sensitivity is higher for gratings in the CF range 11–16 Hz (eg fig 8). At CFs < 11 Hz, peak sensitivity shifts to higher spatial frequencies. This is demonstrated by the progressive sensitive cell, DNIV₁ and the regressive cell DNV₁ (fig 7b).

In summary, the DNs all respond maximally to wide-field motion over the compound eye; their responses are directionally selective with fairly broad tuning; are CF-dependent; non-habituating and adapt to continued motion stimuli in a way that depends upon CF (Fletcher, 1984; Pomfrett, 1987; Ibbotson, 1989; Goodman *et al*,

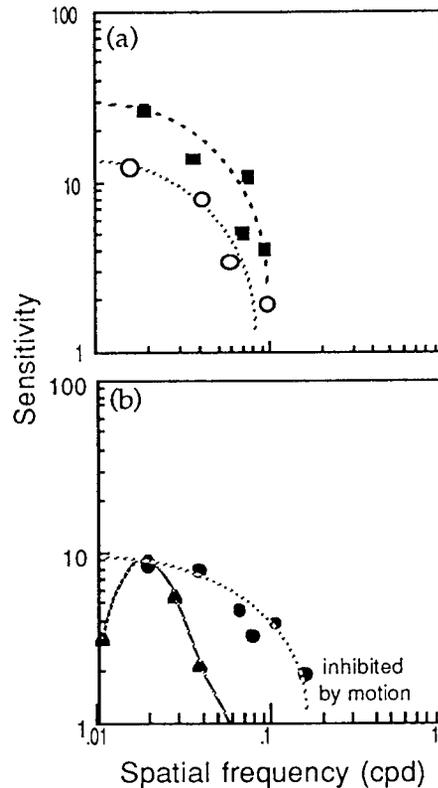


Fig 7. Contrast sensitivity functions for 2 horizontally sensitive cells for gratings moving over the frontal region of the field. **(a)** The sensitivity of DNIV₁ to gratings generating CF 3 Hz (circles) and CF 11 Hz (squares). **(b)** The sensitivity of DNV₂ to gratings generating CF 3 Hz (circles) and CF 114 Hz (triangles).

1987, 1990). In addition, the tuning of their directional responses is biased along one of the orthogonal orientations aligned to the vertical and horizontal. The DNs tend to display similar spatial frequency sensitivities; and their response depend upon the luminance contrast of the stimulus,

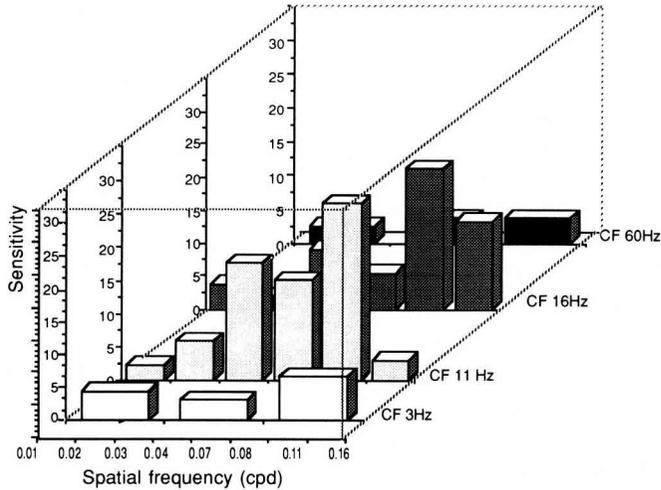


Fig 8. The spatial temporal sensitivity surface of DNII₂ shown by the relationship between spatial and temporal sensitivity functions for gratings moving upwards over the frontal regions of the compound eyes. Each row plotted is the sensitivity to motion as a function of spatial frequency found at one of 4 different temporal frequencies.

which in most cases increases as a function of $|\partial|^2$. On the basis of behavioural experiments the pathway thought to subserve the optomotor response also displays these features. Optomotor responses are compensatory so that the following movements of the head and/or body tend to reduce wide-field optical flow over the retina. Freely flying honeybees elicit such compensatory movements provided that motion fills enough of their visual field and the motion is within a certain range of speeds. Flying bees will follow moving patterns upwards or downwards, to the left or to the right, about their longitudinal or dorso-ventral axis, depending upon the degree of motion experienced (eg Srinivasan and Lehrer, 1984). The optomotor yaw response of tethered bees has been measured (Künze, 1961) and co-

incides with the temporal frequency domain of the responses of the DNs.

ARE THERE DIFFERENCES IN THE PROPERTIES OF THE DNs THAT INDICATE THAT THEY MIGHT BE TRIGGERED BY SPECIFIC OPTICAL FLOW TEMPLATES?

There is no distinct fractionation of the spatial and temporal frequency ranges of the DNs; however certain properties suggest that the DNs differ in their sensitivity to contrast and motion information. For example, one cell, DNIII₄, displays greater sensitivity to high spatial frequencies. Its directional properties recommend it for a role in the control of translatory flight speed and it appears to show a relatively greater re-

sponse to higher contrast frequencies than the other DNs (Ibbotson, 1991). This might indicate a distinction between pathways implicated in different aspects of visually mediated flight control (eg Srinivasan *et al*, 1993).

It has been suggested that the wide extent of an insect's field of view (313° around the horizontal plane of the honeybee: Seidl and Kaiser, 1981) allows the detection of optical flow templates which may occur at certain locations and which correspond to specific types of self and object motion (Horridge, 1992). Certain behaviours exhibited by insects do suggest that they might be triggered by specific sorts of optical templates, for example, detecting targets which elicit responses such as landing (eg *Musca*: Wagner, 1982) chasing (eg tsetse fly: Brady, 1991) or escape (eg *Musca*: Holmqvist and Srinivasan, 1991). It is legitimate to ask whether the properties of the DNs provide some evidence for the detection of specific optical flow templates. As output neurons they are probably the point(s) of convergence for the neural substrate underlying different motion-sensitive behaviours and as such should form a good probe to enquire about the substrate(s) which extract specific features from image flow.

Two stimulus regimes have been used to examine whether the DNs have the capacity to extract specific types of information from the motion of the visual surround and whether this sort of information could indicate particular flight scenarios. The first stimulus regime simulated motion over the lateral regions of the eyes. Synchronous motion of gratings in similar or opposite directions were used to mimic the optical flow consistent with roll, pitch and yaw (Pomfrett, 1987). This revealed that the DNs were tuned to particular sorts of simulated motion (Goodman *et al*, 1990; Ibbotson, 1990, 1991; Ibbotson and Goodman, 1990). Some neurons respond preferential-

ly to upward or downward motion over the frontal region of the eyes, which would enable them to signal deviations in pitch or altitude, for instance if the honeybee were to involuntarily dive or lift (eg DNI; fig 1b). Other DNs also respond to vertical motion, but are more sensitive to upward or downward motion in opposite directions over the lateral regions of the eyes and are therefore suitable for reporting rotations about the longitudinal body axis, for instance during roll (eg DNIV₂; fig 1a,b). Some of the DNs respond maximally to rotations about the dorso-ventral axis of the bee (eg DNVII; fig 1d). This sort of horizontal selectivity yields the capacity to signal motion in the yawing plane, as when deviating from a straight forward course. Yet another DN is sensitive to progressive horizontal motion over the eyes (eg DNIII₂; fig 1c,d). Such optical flow arises in forward translations and might indicate a role in registering changes in flight speed (Ibbotson, 1991).

The distribution of information conveyed by the DNs in the thoracic ganglia is consistent with the coordinated changes in the muscular activity required for particular sorts of compensatory movements. For instance, DNs sensitive to pitch distribute their information symmetrically to both halves of the pro-thoracic and mesothoracic ganglia. This permits symmetrical changes by the motor system, and might be analogous to the bilaterally distributed branches of pitch-sensitive neuron, DNM, in the locust (Griss and Rowell, 1986; Rowell and Reichert, 1986). Course deviations rarely have perfect symmetry and the correction of roll (Srinivasan, 1977) and yaw deviations (Götz *et al*, 1979) require an asymmetrical change in muscular activity on either side of the body. The 3 roll-sensitive DNs confine their arborisations to one half of the thoracic ganglia and as one of them crosses the brain, descending into the thorax on the

opposite side of the body, each half of the thorax would receive data about roll to the right or to the left. Since each half of the ganglia also receives pitch information, specific types of deviation could be identified by the thoracic interneurons/motoneuron pool. By comparing the signals derived from both sides, banking turns for instance, could be distinguished from rotation about the horizontal or the longitudinal axes. Correctional movements of the head or whole body, counteracting yaw about the longitudinal axis, also require asymmetrical change in muscular activity on each side of the body (Götz *et al*, 1979). The arborisations of the yaw-sensitive DNs are also confined to one side of the ganglia, and again collectively these cells would inform each half of the thorax that course deviation to the right or left had occurred.

DIFFERENT COMBINATIONS OF HORIZONTAL OPTICAL FLOW

Of 19 physiologically characterised identified DNs, 11 respond preferentially to motion along the horizontal (Bidwell, 1992). A second set of experiments examined the effect of particular combinations of horizontal optical flow (figs 8, 9). The frontal regions of the visual field were examined since objects are fixated there in honeybees (Lehrer, 1990; Zhang *et al*, 1990) and this region may be more effective in mediating landing (*eg* flies: Fischbach, 1983). The regime consisted of the independent stimulation of each eye with horizontally moving gratings. The first 4 stimuli in a sequence of 6 were progressive or regressive motion of gratings over the contralateral and then the ipsilateral eyes. The last 2 stimuli in the sequence simulated contraction and expansion of the flow field from a point in the centre of the monitor. These entailed progressive motion over

the ipsilateral eye synchronous with regressive motion over the contralateral eye and regressive motion over the ipsilateral eye synchronous with progressive motion over the contralateral eye respectively. This resembles some of the components of the flow field arising during stable translation when flow occurs between 2 poles of no motion lying at opposite ends of the line of the bee's direction of flight. In forward translation the flow field expands out from the pole in front and contracts into the pole to the rear of the insect. Thus in the frontal region of the visual field optical flow caused by straightforward translation will be in opposite directions either side of a vertical plane formed by the dorso-ventral axis and the anterior-posterior axis of the head. Optical flow expands from a pole in the frontal regions of the field during normal forward flight and is approximately horizontal around the equatorial plane of the eye (Horridge, 1992).

Generally, the horizontally tuned DNs are more sensitive to expanding rather than contracting optical flow in the frontal field. It would seem that collectively the responses of the DNs are better suited to detect templates representing the forward motion of the honeybee. This agrees with the view that the underlying network has evolved to extract information from the optical flow expected for the normal flight of the insect, which for the honeybee is forwards. Like other insects (*eg Drosophila*: David, 1982) the honeybee promotes a constant preferred angular velocity of progressive optical flow over both eyes by altering the power output of the wings (Esch *et al*, 1975). This enables the bee to stabilise her forward course and avoid crash landing. It also provides the appropriate optical flow required for searching and scanning and enables the honeybee to maintain a constant body orientation, for example when hovering during fixation of a landing site (*eg* Wehner, 1981).

Insects can maintain a constant position in space by using the velocity and position components of the flow field. For example, *Trigona* guard bees hover when station-keeping by altering their distance from the hive entrance rather than their orientation relative to it (Zeil and Wittmann, 1989). In flight, honeybees also demonstrate that their forward speed is affected by the velocity of optical flow (Hodson, personal communication). The effect upon the flight speed of bees trained to visit the centre of a spiral pattern (devised by Braitenberg and Taddei-Ferretti, 1966; Taddei-Ferretti and Perez de Talens, 1973) depends upon whether its movement creates apparent contraction or expansion. The influence of optical flow upon the honeybee's forward speed is particularly evident for contracting flow at certain velocities (Hodson: personal communication). As the honeybee makes her approach to a landing site, over the last 1 M the optical flow in the frontal field has a mean progressive velocity of $110^\circ/\text{s}$ in opposite directions over the fronto-lateral regions of both eyes. Contracting spirals which generate temporal frequencies of 9.5 Hz and an apparent regressive velocity of $120^\circ/\text{s}$ elicit a dramatic increase in the bee's forward velocity to $250^\circ/\text{s}$. This suggests that when the bee is flying towards her landing site the preferred progressive motion over the front-lateral regions in each direction is maintained around $100^\circ/\text{s}$. In general at progressive velocities of around $110^\circ/\text{s}$, more of the neurons (DNs, IV_1 , IX , III_1 and III_4) linearly integrate the monocular components of the binocular stimuli in their response to expansion than they do in their response to contraction (eg DNI_1 , fig 9c). When CF is constant, DNI_1 's linearity for the integration of the monocular components of the expanding stimulus decreases with increasing spatial frequency (or decreasing velocity). Since linearity decreases with CF (or increasing velocity)

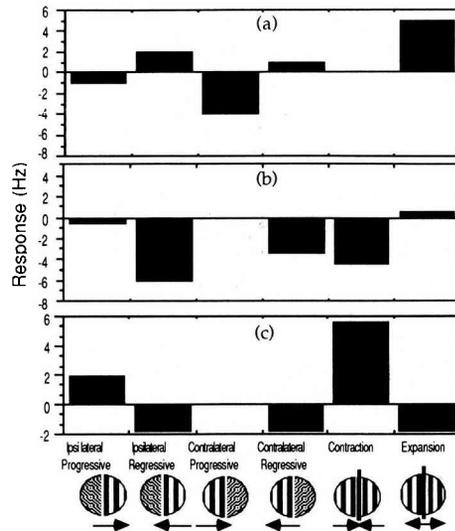


Fig 9. The responses relative to baseline firing of (a) $DNIII_4$; (b) DNV_1 and (c) DNI_1 to monocular progressive and regressive motion over the ipsilateral and contralateral eyes, and to the binocular combination of these in simulated contraction (ipsilateral regressive and contralateral progressive) and expansion (ipsilateral progressive and contralateral regressive). The spatial and temporal frequency of the gratings were set at the optimum values for the cell responses at 0.019 cpd and 11 Hz respectively. $DNIII_4$ (a) responds more strongly to expansion than expected from the sum of the responses to ipsilateral progressive and contralateral regressive motion. DNV_1 (b) responds to expansion and contraction approximately equal to the sum of the responses to the monocular components of these stimuli. DNI_1 responds more strongly to contraction than expected from the sum of the responses to ipsilateral regressive and contralateral regressive motion.

when spatial frequency is constant, this suggests that any velocity dependence occurs only outside the peak CF range, with greater linear integration at low velocities.

The responses of 2 contralaterally descending cells DNIII₄ and DNVI₁, to the different combinations of horizontal flow have been examined in particular detail. The directional selectivities of these 2 cells suggest that they would be equally suited for the detection of frontal motion information as well as motion over the lateral field. On the basis of their expansion and contraction ratios (figs 8, 9) DNs VI₁ and III₄ represent opposite extremes in the way that they integrate the monocular components of the contracting and expanding stimuli. They also differ in the degree to which spatial and temporal frequency affects the integration of the monocular components of expansion and contraction. Unlike DNVI₁, DNIII₄ approximately linearly integrates expansion and inhibits contraction regardless of the spatial or temporal frequency of the stimulating gratings. The binocular integrative properties of DNIII₄ for the lateral regions of the eye support it as a candidate cell in the substrate subserving the control of translatory flight (eg Ibbotson, 1991). Such a substrate might in turn contribute to the landing scenario in the honeybee. DNIII₄ belongs to the only group of cells that demonstrate a selectivity for bilateral progressive motion over the lateral regions of the eye, in contrast to DNVI₁ for example, which shows a strong response to yaw. Whilst both DNIII₄ and DNVI₁ descend contralaterally, their anatomy shows them to be very different. For example, DNVI₁ has highly diffuse arborisations throughout both sides of the brain whilst DNIII₄ restricts its field predominately to a small area on the ipsilateral side. In the thorax, DNVI₁ restricts its outputs to one side of the thoracic ganglia and group III DNs extend to cover both sides. Translatory flow might well be integrated by the same neurons that control steering. But under certain circumstances such as landing, an explicit translatory template is essential in order to modulate muscular ac-

tivity on each side of the insect symmetrically. Functional specialisation of steering muscles has been clearly demonstrated in studies on *Drosophila* (Waldvogel and Bausenwein, 1991) and *Musca* (Egelhaaf, 1989). Different steering muscles mediate different behavioural response components during object orientation, optomotor yaw control and landing and presumably receive inputs from pathways selectively tuned to specific sorts of motion. DNIII₄ is the only neuron tested which consistently integrates expansion in a nearly linear fashion and strongly inhibits contraction (fig 9a). Thus the overall spatial integration properties of DNIII₄ recommend it for a role in landing. The honeybee does not display the stereotypical response of landing as does the fly (Bidwell and Goodman, personal observation), but neither is she constantly airborne. So her deceleration prior to landing might rely on similar optical templates to those that control fly landing. The response associated with landing in flies is reflexive, and released by striped patterns with progressive bilateral motion (Eckert, 1984; Borst and Bahde, 1986, 1987) and centrifugal motion in front of the fly (Goodman, 1960; Perez de Talens and Taddei-Ferretti, 1970; Wehrhahn *et al*, 1981; Eckert, 1984).

An integration model has been proposed to account for landing in flies. It operates upon signals from direction-sensitive elementary movement detectors (EMDs: eg Borst and Egelhaaf, 1989), conceivably with the physical identity of those mobilised in optomotor responses (Borst and Bahde, 1986). In this model the output of the EMDs is spatially and temporally summed by a leaky integrator (Borst and Bahde, 1986) and then processed by a threshold device which determines whether landing occurs or not (Borst and Bahde, 1986, 1987, 1988; Borst, 1989; Rees and Spatz, 1989). Pooled spatially, the movement signal increases with the apparent

size of the landing site or the number of stimulated detectors. Pooled temporally, the landing distance will depend upon the distance from which the fly approaches the landing site. A threshold temporal integrator requires the gradual buildup of signals to a critical value, thus a prerequisite of candidate cells is a gradual rise in firing rate. DNIII₄ requires a relatively long time (270 ms) to reach 75% of its maximum firing frequency compared to DNVI₁, which reaches the same relative firing level in the shortest time (75 ms). In order to prevent a landing response in mid-air when the integrator is filled, the input channels to the landing integrator should switch themselves off if stimulation is weak. The DNs have been described as either phasic or tonically responding (Bidwell, 1992; Ibbotson, 1992). By extrapolating from the exponential decay of the spike frequency measured in 100 ms bins to the point where the response is equal to $1/e$ x maximum firing frequency, it was found that DNIII₄ was more phasically responding than DNVI₁. Thus DNIII₄, which adapts to progressive motion much more rapidly (where the exponential decay of the response at $1/e$ is 580 ms) than DNVI₁ (where the exponential decay at $1/e$ is 825 ms) would be better suited to playing a role in the integration mechanism which may control landing.

DNVI₁ would be better suited to the continual monitoring of optical flow. It has many blebbed outputs in the suboesophageal ganglion where it might directly impinge upon the dendrites of neck motor neurons (eg Pomfrett, 1987). Head movements are often found in the control of yawing deviations in flying insects (eg Hengstenberg *et al*, 1986; Hensler, 1988; Hensler and Robert, 1990). They are also made by insects when extracting distance information (eg locust: Wallace, 1959; Collett, 1978; Collett and Patterson, 1990; crickets: Goulet *et al*, 1981). Honeybees

can use motion parallax in figure-ground discrimination to detect a landing site (Srinivasan *et al*, 1989). Thus it is possible that the response of DNVI₁ might detect a template used to modulate the orientation of the head towards the sort of motion border which indicates the edge of a landing site. In this sense this would reflect the inclusion of information processed by a motion parallax subsystem.

Motion parallax can reveal information about the structure of the world (eg Lehrer *et al*, 1988) which is essential to the honeybee in the visual mediation of translatory flight. The velocity profile of the honeybee's world as she flies is 'inhomogeneous' (Buchner, 1984). The component retinal velocities generated in forward flight differ in their direction and size with respect to the parts of the eyes subtending them and due to the distance of objects from the bee and their distribution in the scene. This means that mechanisms which control translatory movements must also incorporate information about the location of the locally defined vectors (Collett, 1980). The second operating rule for optomotor control proposed by Collett (1980) suggests that the control of forward thrust might be accomplished by a separate optomotor pathway to the classical one which compensates for changes in flight course. If this is the case then it is possible that some of the DNs might receive optomotor information *via* different processing pathways. There is a degree of individuality for the different DN with respect to how their responses to the combinations of horizontal flow are integrated between the 2 eyes and how they depend on spatial and temporal frequency (eg DNIV₁; fig 10). The DNs also display heterogeneity in other details of their characteristics, for example the time courses of their responses (figs 2b, 3b, 4b) and in some cases their contrast characteristics (fig 5a-c). It is thus conceivable that some of the indi-

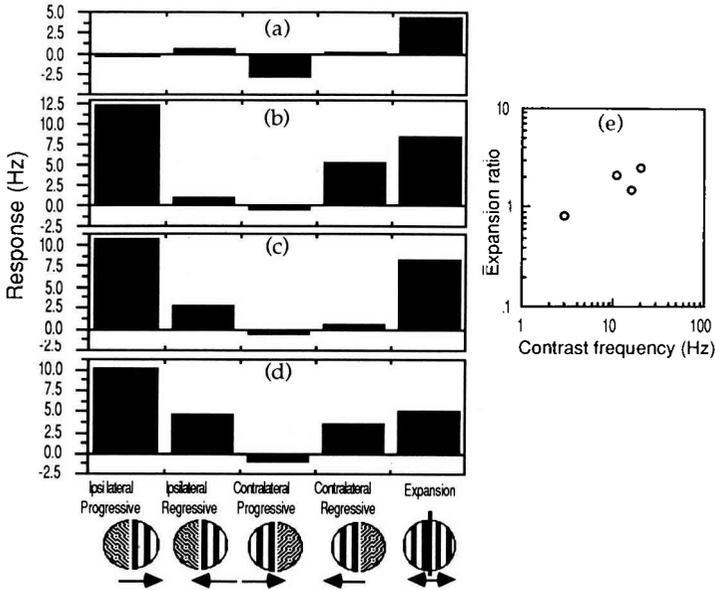


Fig 10. The responses of DNIV₁ to monocular progressive and regressive motion over the ipsilateral and contralateral eyes, and to the binocular combination of ipsilateral progressive and contralateral regressive in simulated expansion. The spatial frequency of the gratings was set at the optimum value of 0.019 cpd. The temporal frequency (CF) of the gratings was varied: **(a)** 3 Hz; **(b)** 11 Hz; **(c)** 16 Hz; **(d)** 20.5 Hz. The response to expansion relative to the response to the monocular components decreases with increasing CF. This is shown by plotting the expansion ratio as a function of CF **(e)** where:

$$\text{Expansion ratio} = \frac{\text{Absolute response to ipsilateral progressive} + \text{absolute response to contralateral regressive}}{\text{Absolute response to binocular expansion}}$$

Values approximating to 1.0 describe a spatially linear relationship between the response to expansion and the sum of the monocular responses. Values > 1.0 demonstrate how the response to the monocular components of expansion is suppressed when they are presented together (see legend to figure 9).

vidual characteristics of the DNs reflect access to features coded previously along pathways parallel to the classic optomotor pathway.

Résumé — Les fonctions possibles d'une population de neurones descen-

dant de la voie optomotrice de l'abeille, *Apis mellifera* L. L'abeille possède plus de 20 inter-neurones descendants (DNs), qui donnent des réponses sur la direction de mouvements à champs larges se produisant au-dessus des yeux composés. Les caractéristiques des réponses de neu-

rones individuels identifiés ont été étudiées à l'aide de grilles à ondes carrées déplacées mécaniquement ou de grilles à ondes sinusoïdales synthétisées électroniquement sur un moniteur X-Y.

La direction du mouvement préférée des DNs peut être décrite comme étant vers l'avant, vers l'arrière, vers le haut ou vers le bas (fig 1, 3, 4). La division physiologique entre cellules sensibles à la verticalité et cellules sensibles à l'horizontalité peut être corrélée avec certaines caractéristiques anatomiques. Il existe 2 groupes distincts de neurones descendants dans le cerveau. Dans chaque groupe, certains DNs préfèrent le mouvement vertical, d'autres le mouvement horizontal. La localisation dans le thorax et la structure des extrémités des cellules sélectives de la verticalité suggèrent que la connexion optomotrice de l'information verticale est plus directe que celle de l'information horizontale. Le maintien de la sélectivité verticale et horizontale à travers le cerveau jusqu'au thorax permet également d'intégrer de façon souple l'information provenant des 2 canaux. Cela peut expliquer la large gamme des spectres de réponse des DNs. Des cellules à spectre étroit ont besoin de plus de temps pour arriver au niveau de réponse maximale que des cellules à spectre large (fig 2b).

La réponse des DNs dépend du contraste de luminance, et elle augmente en fonction de $dI2$ (fig 5a, b). Les fonctions de sensibilité au contraste (CSFs) ont été utilisées pour déterminer l'étendue des fréquences spatiales que le système utilise pour coder le mouvement. Les optimums de fréquence spatiale pour le déplacement des grilles de fréquence temporelle optimale se situent entre 0,03 et 0,06 cycles par degré (fig 6b). Cette étendue est comparable à celle des optimums de fréquence spatiale pour les cellules analysées auparavant dans la voie visuelle d'insectes tels que les mouches ou les papillons.

Pour une luminance moyenne plus faible la fréquence spatiale du pic prend des valeurs plus faibles (fig 6b). Pour des fréquences temporelles plus faibles, la sensibilité du pic passe à des fréquences spatiales plus élevées (fig 7b).

L'examen des réponses des DNs aux combinaisons de mouvement dans les différentes directions au-dessus de chaque œil suggère qu'elles transmettent des motifs spécifiques. Les grilles à ondes carrées ont été utilisées pour imiter le flux optique conformément au roulis, au tangage ou aux embardées. Cela montre que les DNs sont sélectifs vis-à-vis de types particuliers de mouvement. Certains détectent des déviations dans le tangage ou l'altitude, d'autres des déviations dans l'axe longitudinal du corps pendant le roulis, et d'autres encore répondent le plus aux déviations de l'axe ventro-dorsal comme dans une embardée.

Les 11 DNs sélectifs de l'horizontalité présentent des différences dans leurs réponses à diverses combinaisons de flux horizontal. Ils n'intègrent pas le flux horizontal au-dessus des 2 yeux de la même façon, et varient aussi en ce qui concerne le nombre de fois où l'intégration dépend de la fréquence spatiale et temporelle (fig 9 et 10). La cellule DNII₄, par exemple, intègre les composantes monoculaires du flux en expansion de façon à peu près linéaire mais supprime sa réponse aux composantes monoculaires du flux en contraction lorsque les 2 flux se présentent ensemble. Cela se produit quelle que soit la fréquence spatiale ou temporelle. Ses propriétés d'intégration spatiale globale, plus sa distribution symétrique de l'information dans le thorax suggèrent qu'elle a un rôle dans le comportement d'atterrissage. Les DNs présentent une hétérogénéité dans les autres caractéristiques, par exemple le temps de réponse (figs 2b, 3b et 4b) et, dans certains cas, leurs caractéristiques de contraste (fig 5a-c). Cela suggère

que les DN's individuels ont accès à des motifs codés auparavant le long des voies parallèles à la voie optomotrice classique.

neurone descendant / vision / sensibilité au mouvement / sélectivité de la direction

Zusammenfassung — Mögliche Funktion einer Population absteigender Neurone in der optomotorischen Leitungsbahn der Honigbiene, *Apis mellifera*.

Die Biene verfügt über mehr als 20 absteigende sensorische Interneurone (DNs), die selektiv gerichtet auf großflächige Bewegungen reagieren. Die Reaktionseigenschaften individueller Neuronen wurden untersucht, wobei entweder mechanisch bewegte rechteckig oder sinusförmig modulierte Streifenmuster benutzt wurden, die elektronisch auf einem X-Y-Schirm erzeugt wurden.

Die bevorzugten Bewegungsrichtungen der DN's können als progressiv, regressiv, aufwärts oder abwärts beschrieben werden (Abb 1, 3 und 4). Die physiologische Einteilung in vertikal- oder horizontal-empfindliche Zellen kann mit bestimmten anatomischen Merkmalen korreliert werden. Zwei deutlich abgegrenzte DN-Gruppen sind im Gehirn vorhanden. In jeder Gruppe treten Neurone auf, die bevorzugt auf vertikale oder horizontale Bewegungen reagieren. Die Lage und Struktur der Endigungen der vertikal-abgestimmten Zellen im Thorax legt die Vermutung nahe, daß die visuell-motorischen Verbindungen für vertikale Bewegungsinformationen direkter sind als diejenigen für horizontale Informationen. Die Beibehaltung der Richtungsselektivität für vertikale und horizontale Bewegungen vom visuellen System bis zum Thorax ermöglicht eine flexible Integration der Bewegungsinformationen. Die breite Richtungsselektivität der DN's und ihre Reprä-

sentation in nur zwei Kanälen könnte von Vorteil sein. Eng abgestimmte Zellen benötigen nämlich längere Zeit, um maximal zu reagieren, als breiter abgestimmte Zellen (Abb 2b).

Die Antwort der DN's hängt vom Helligkeitskontrast ab. Gewöhnlich nimmt die Reaktion als eine Funktion von dI_2 zu (Abb 5a, b). Funktionen der Kontrastempfindlichkeit (CSFs) wurden benutzt, um die Empfindlichkeit der Neuronen für verschiedene räumliche Frequenzen der Streifenmuster zu bestimmen. Bei bester zeitlicher Frequenz (11 Hz) liegen die Optima für verschiedene räumliche Frequenzen sich bewogender Streifenmuster zwischen 0,03 und 0,06 Umwendungen per Grad (Abb 6b). Diese Bandbreite steht in guter Übereinstimmung mit den Optima der Raumfrequenzen von Zellen, die früher im visuellen System anderer Insekten wie Fliegen und Schmetterlingen gefunden wurden. Bei niedrigerer mittlerer Helligkeit wird das Optimum für Raumfrequenzen zu niedrigeren Werten hin verschoben (Abb 6b). Bei niedrigeren zeitlichen Frequenzen wandert der Gipfel der Empfindlichkeit zu höheren räumlichen Frequenzen (Abb 7b).

Die Antworten der DN's auf Kombinationen von Bewegungen in verschiedenen Richtungen legen nahe, daß die DN's auf spezifische Grundmuster von Bewegungsreizen reagieren. Rechteckförmige modulierte Streifenmuster wurden benutzt, um die optischen Grundmuster zu simulieren, die bei Bewegungen des Tieres während des Rollens, Neigens und Gierens (seitliche Versetzung) entstehen. Es zeigte sich, daß die DN's auf besondere Bewegungstypen abgestimmt sind. Einige erkennen Änderungen in der Neigung oder Höhe, einige reagieren auf Änderungen, wie sie beim Rollen um die Körperlängsachse auftreten, und andere reagieren am stärksten auf Abweichungen um die dorsoventrale Achse wie beim Gieren.

Die 11 horizontal-abgestimmten DNs zeigen Unterschiede in ihrer Antwort auf unterschiedliche Kombinationen der Horizontalen Bewegung von Streifenmustern. Sie integrieren die horizontale Bewegung über die beiden Augen nicht in derselben Weise und sie unterscheiden sich auch darin, wie die Integration von räumlicher und zeitlicher Frequenz abhängt (Abb 9 und 10). Die Zelle DNIII4, zB integriert die monokularen Komponenten eines expandierenden Bewegungsreizes ungefähr linear, aber sie unterdrückt ihre Antwort auf die monokulare Bewegungskontraktion, wenn beide Reize zusammen präsentiert werden. Dies geschieht unabhängig von der räumlichen und zeitlichen Frequenz. Ihre Eigenschaften der räumlichen Gesamtintegration, zusammen mit der symmetrischen Verteilung der Information im Thorax, legen eine Rolle dieses Systems beim Landeverhalten nahe. Die DNs zeigt Heterogenität bei anderen Merkmalen, zB beim zeitlichen Verlauf der Antwort (Abb 2b, 3b, 4b) und in einigen Fällen bei ihrer Kontrastempfindlichkeit (Abb 5a–c). Dies legt die Vermutung nahe, daß individuelle DNs mit visuellen Neuronen verschaltet sind, die andere Eigenschaften der visuellen Stimuli kodieren und parallel zu den klassischen optomotorischen Bahnen verlaufen.

Absteigende Neurone / Visuelles System / Bewegungsempfindlichkeit / Richtungsempfindlichkeit

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