

SHORT COMMUNICATION

A MOTION-SENSITIVE VISUAL DESCENDING NEURONE IN
APIS MELLIFERA MONITORING TRANSLATORY FLOW-
FIELDS IN THE HORIZONTAL PLANE

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Behavioural studies in insects have shown that simulated rotations of the visual panorama in the yaw, roll and pitch planes lead to optokinetic responses which, under natural conditions, counteract involuntary rotations of the body and thus maintain a stable visual orientation. Electrophysiological investigations have found neurones that respond selectively to rotatory motion in these planes. This evidence, in conjunction with lesioning and electrical stimulation studies, has led to the hypothesis that these rotation-sensitive neurones control optokinetic responses (for a review, see Hausen and Egelhaaf, 1989). Two other types of visually induced behaviour, landing responses and the control of forward flight speed, rely on the detection of translatory rather than rotatory visual flow-fields. For example, it has been shown that flight speed is controlled in insects by adjusting the power output of the wings such that there is a constant preferred angular velocity of image flow from front to back (progressive motion) over both eyes (*Apis mellifera*: Esch *et al.* 1975; *Drosophila melanogaster*: David, 1982). Similarly, landing responses can be induced in flies by moving visual images progressively over both eyes (Eckert, 1984). In spite of these behavioural data there is little evidence, except for a few preliminary reports (Baader, 1988; Rowell, 1989), of neurones that monitor translatory flow-fields, i.e. cells that are maximally sensitive to motion in the same direction over both eyes and not sensitive (or less sensitive) to rotatory motion.

The present investigation studied the responses of descending neurones in *Apis mellifera* using two large visual patterns (each subtending an angle of 120°), mounted on each side of the head, such that the centre of each pattern was aligned with the horizontal axis of the head. The patterns consisted of black and white square-wave gratings (Michelson's contrast 0.80) with spatial periods of 15° or 20° at the closest distance to the eyes. The patterns could be moved back and forth through the visual field using variable-velocity servo motors and could be rotated

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about their centre points, between each presentation of the moving pattern, using stepper motors. This arrangement allowed the patterns to be moved in any direction throughout the lateral visual fields of the eyes either independently or together. When moved together the patterns could be used to simulate rotatory or translatory flow-fields (for details see Ibbotson and Goodman, 1990). This type of investigation combined with intracellular recording and subsequent ionophoretic injection of neurological stain (cobalt chloride) has led to the identification of a descending neurone (DN) that responds predominantly to the progressive motion of a horizontal flow-field.

The identified neurone has extensive spine-covered branches in the ipsilateral side of the brain, i.e. the side in which the cell body is located (Fig. 1A). These branches invade the dorsal surface of the brain in the regions occupied by the terminals of several horizontal-motion-sensitive lobula output neurones (Ibbotson, 1991). The dendritic branches of the DN also invade more ventral regions of the brain such as the anterior optic tubercle. The soma of the neurone is located in the dorsal cell body rind. The cell crosses the brain above the oesophageal foramen, the axon narrowing in this region from a diameter of $5\ \mu\text{m}$ to $2\ \mu\text{m}$. As the axon enters the contralateral brain it expands again to $5\text{--}8\ \mu\text{m}$ and descends into the ventral nerve cord. As it does so it gives off many beaded axon collaterals that spread throughout the contralateral deutocerebrum. The cell travels through the ventral nerve cord to its terminals in the posterior thoracic ganglion. The cell gives off numerous bead-covered branches *en route*. These branches invade both lateral and medial regions of the contralateral ganglia. This neurone belongs to a cluster of at least four DNs that have very similar brain anatomies. The cluster of four cells has been stained in mass fill preparations on 23 occasions and the cells have been stained as single fills in five brains. The shape of the neurites and the fine structure of the dendritic branches does vary slightly from preparation to preparation, but the structure of the main axon and the areas of the brain occupied by the dendrites and the cell bodies show no significant variability.

Recordings from one anatomically identified and three unidentified flow-field-sensitive neurones have shown that the cells give a broadly tuned, direction-

Fig. 1. (A) *Camera lucida* drawing from a whole-mount preparation of a predominantly translational flow-sensitive descending neurone. The cell has spine-covered arborizations in the ipsilateral brain and blebbed arborizations in the contralateral brain. The cell gives off numerous bleb-covered branches in the thoracic ganglia. These invade the motor neuropile in the dorsal and medial regions of the ganglia. (B) Directional tuning of the neurone as tested at an angular velocity of 90°s^{-1} . The responses to monocular stimulation of the ipsilateral (○) and contralateral (□) eye and to translatory stimulation of both eyes (●) and to rotatory stimulation of both eyes (■) are shown. Mean values derived from one identified cell ($N=3$). Responses in spikes s^{-1} ; $0\ \text{spikes s}^{-1}$ is the mean resting activity. (C) The velocity-tuning characteristics of the neurone recorded in B. Mean values \pm s.d. ($N=4$). P and R indicate progressive and regressive motion in the horizontal plane over the lateral visual fields of the eyes; OF, oesophageal foramen; SOG, suboesophageal ganglion; PRO, prothoracic ganglion; MESO, mesothoracic ganglion; META, metathoracic ganglion.

selective response to motion, the maximal response to monocular stimulation in the lateral regions of each eye being evoked by progressive motion in the horizontal plane (Fig. 1B). Motion in the regressive, null direction over either eye reduces the resting activity of the cells and hence evokes an inhibitory response. When the patterns were moved simultaneously from front to back over both eyes, simulating forward movement of the insect, the inputs from the two eyes summated to give responses that were approximately 20–30% larger than the

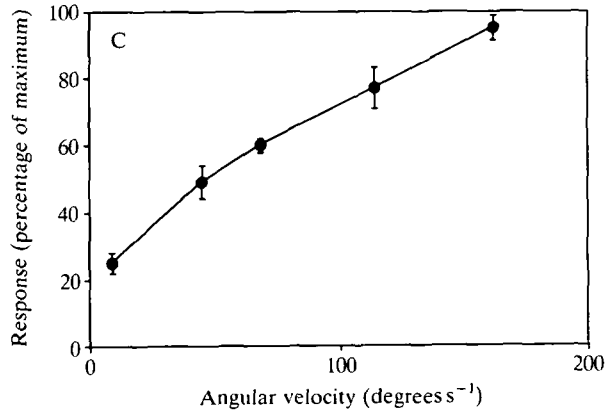
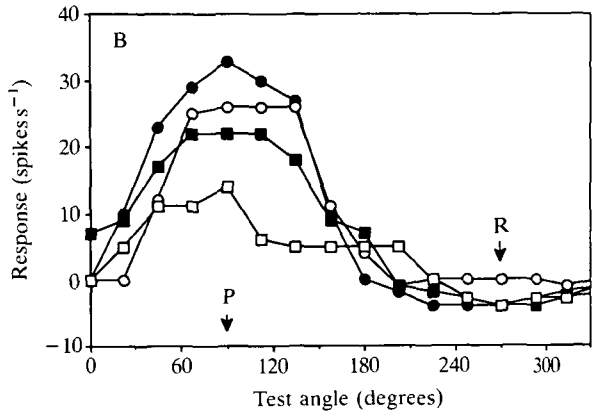
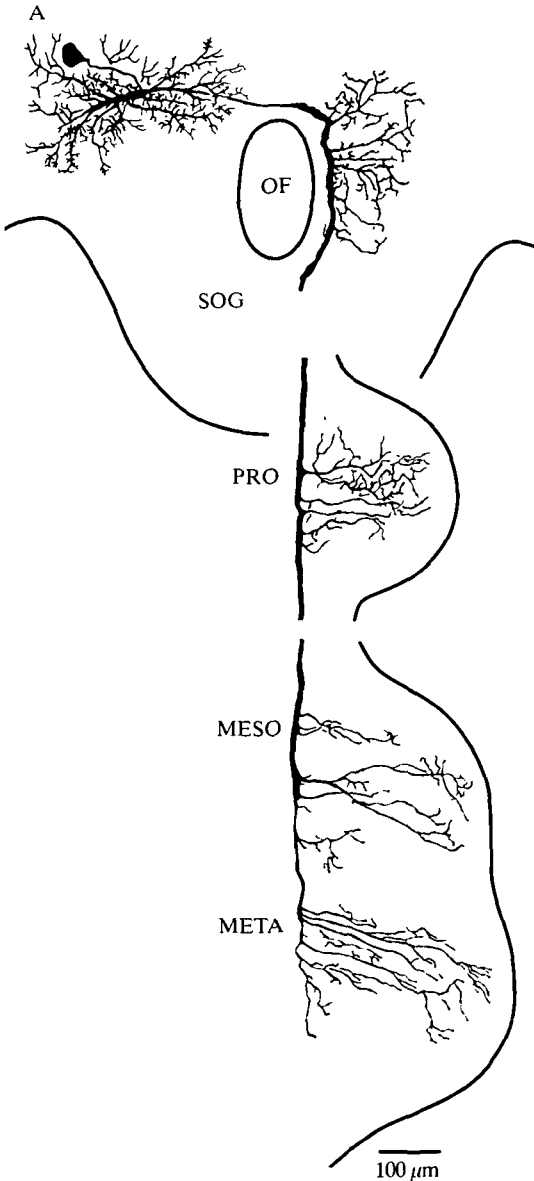


Fig. 1

responses to ipsilateral stimulation alone (Fig. 1B). Simultaneous regressive motion over both eyes led to a large inhibitory response. Simulated rotatory motion, where there was progressive motion over the ipsilateral eye and regressive motion over the contralateral eye, led to a response that was smaller than the response to monocular stimulation of the ipsilateral eye (Fig. 1B). Simulated rotatory motion in the opposite direction induced an inhibitory response from the cells. The contrast frequency tuning curve of the one neurone tested showed a gradual increase in response from 0.5 to 8.5 Hz (Fig. 1C). No optimum value was found in this range, which equated to angular velocities of $10\text{--}160^\circ\text{s}^{-1}$. The receptive field of the neurone was not examined in detail, but preliminary examinations with a hand-held grating pattern elicited responses, from the four cells tested, to progressive motion in the dorsal, equatorial and ventral areas of the lateral visual field.

In summary, the cell described is maximally sensitive to horizontal motion in the lateral regions of the eyes. Horizontal progressive motion in the lateral eye regions is a powerful stimulus for eliciting landing responses in flies (Eckert, 1984) and has been shown to have a strong influence on visual orientation behaviour and air speed control in free-flying honeybees (Srinivasan, 1989), locusts (Rowell, 1989) and *Drosophila melanogaster* (David, 1982). As the terminal branches of this descending neurone are located amongst the flight-motor neuropile of the thoracic ganglia and the cell responds predominantly to translatory flow-fields, it could have a role in controlling such types of behaviour. The directional tuning properties of the neurone show that it is sensitive to rotatory motion as well as translatory motion, although the latter is a more powerful stimulus. Other horizontally tuned DNs in the bee are also sensitive to both rotatory and translatory motion in the horizontal plane; however, these are more sensitive to rotatory motion (Ibbotson and Goodman, 1990; Ibbotson, 1991). It is possible that the presence of two sets of cells, each type with a different bias for translatory and rotatory motion, reflects the need for fine adjustments in the visual processing underlying course control. Descending neurones sensitive to progressive translatory motion in the locust have also been found to give at least some response to rotatory motion (Baader, 1988). Indeed, in the translatory-motion-sensitive locust DNs the responses to rotatory motion were enhanced when a progressing flow-field was superimposed on the rotatory stimulus. The results suggest an interaction between the predominantly rotatory and translatory DNs that enhances the specificity of the motor responses to the visual stimulus. It is possible that the neurones that are postsynaptic to the pair of predominantly flow-sensitive DNs are able to eliminate the rotatory component of the response through such an interaction.

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