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Evidence for velocity-tuned motion-sensitive descending neurons in the honeybee

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Behavioural experiments suggest the existence of two functionally distinct movement-sensitive pathways in honeybees: one mediates optomotor behaviour, consisting of reflexive turning responses preventing deviations from course, and the other controls flight speed. The first consists of direction-selective neurons responding optimally to a particular temporal frequency of motion, regardless of the pattern's spatial structure. The temporal frequency dependence matches the temporal tuning of the optomotor output. Behavioural experiments suggest the second pathway contains velocity-tuned cells, which generate equal-sized responses for any given image velocity, for patterns with a range of spatial structures. Here, recordings were made from direction-selective neurons in the honeybee's ventral nerve cord. Neurons were tested for responses to motion at velocities of 40–1000 deg s^{-1} using four gratings with spatial periods of 11–76°. In addition to temporal frequency-dependent optomotor neurons, direction-selective cells were found that had the same shaped velocity–response functions for all four patterns. The velocity-tuning properties of these cells suggest a possible role in monitoring flight speed because their velocity tuning matches the image velocities encountered during free flight and landing behaviour.

Keywords: visual descending neuron; velocity tuning; insect vision

1. INTRODUCTION

For insects, the optic flow (Gibson 1950) generated on both retinas during locomotion has an important role in the control of body orientation (e.g. Wehner 1981), gaze stabilization (Hengstenberg 1991; Hengstenberg *et al*. 1986) and flight speed—e.g. studies on bees (Esch *et al*. 1975; Srinivasan *et al*. 1996) and flies (David 1982). The stabilization of flight attitude is mediated by optomotor responses, which are turning responses that stabilize flight direction against gusts of wind or other outside factors. A consistent feature of optomotor responses is that, when the stimulus is a moving periodic grating, the sizes of the behavioural turning responses are dependent on the temporal frequency of the pattern. Temporal frequency is the number of cycles of the periodic pattern to move across a point on the retina per second (image velocity/spatial period). The neural substrate that controls optomotor responses is very well known in a wide range of insects, such as flies (Hausen 1984; Krapp 2000) and bees (Ibbotson 1991*a*). Importantly, the responses of the neurons controlling optomotor responses are dependent on temporal frequency, thus matching the dependency of the behavioural output (for example, see Götz (1964) and Hausen & Wehrhahn (1989) on flies and Kunze (1961) on bees).

In contrast to optomotor responses, insects control forward flight speed using the velocity of the image on their retinas rather than the temporal frequency (von Gavel 1939; David 1982; Srinivasan *et al*. 1996). David (1982) designed a wind tunnel that was lined on its inner walls with a helical barber's pole pattern of black and white stripes. The tunnel could be rotated around its longitudinal axis to generate an apparent axial movement of the patterns along the tunnel. *Drosophila* flew at a speed that generated a constant angular velocity of image movement over their retinas. By changing the width of the stripes in the tunnel, David was able to show that the flies controlled their forward speed using the angular velocity of the image motion and not the temporal frequency. Srinivasan *et al*. (1996) showed that when bees fly through a tapered tunnel they reduce their flight speed as the tunnel narrows, thus keeping the image velocity on the eyes constant. On the other hand, when flying through a tunnel of constant width, they maintain constant flight speed even when the spatial texture on the walls is changed abruptly halfway along the tunnel. This evidence suggests that bees, like *Drosophila*, are able to measure the angular velocity of the image, regardless of its spatial structure. When bees fly through a tunnel lined with striped patterns, they fly along the midline of the tunnel, even when the spatial periods of the stripes on the tunnel walls are different (Srinivasan *et al*. 1991). When one wall is moved in the same direction as the flying bee, while the other wall is held still, the bee flies closer to the moving wall. Conversely, when the wall is moved in the opposite direction, the bee flies closer to the stationary wall. This phenomenon still occurs when the spatial periods of the stripes on the two walls are different. Again, these experiments demonstrate that the bees are inferring range from the absolute retinal image velocities. The present paper records the responses of neurons in the honeybee that are velocity tuned and discusses the possibility that the cells might be involved in controlling velocity-dependent visual behaviour.

2. METHODS

In this study I recorded the responses of neurons in the ventral nerve cord of the honeybee (*Apis mellifera*) to the movements of four striped patterns with spatial periods of 11°, 19°, 38° and 76° (contrast 80%). The patterns were square-wave gratings printed on paper and attached to the outer surface of a revolving drum (100 mm diameter, 110 mm length), which was

driven by a variable velocity DC motor (also see Ibbotson & Goodman 1990). The outer surface of the drum was positioned 30 mm from the bee's eye(s). The drum could be positioned either frontally (stimulating both eyes simultaneously) or laterally (stimulating the left eye only). The drum speed could be varied to give image velocities of 40–1000 deg s^{-1}. The temporal frequency ranges for the fundamental spatial frequency of the stimuli were: 3.6–91 Hz (11° pattern), 2–53 Hz (19° pattern), 1–26 Hz (38° pattern) and 0.5–13 Hz (76° pattern). Between presentations of the moving pattern, the drum could be rotated manually about the animal's longitudinal axis (for frontal stimulation) or the transverse axis of the head (for lateral stimulation) in steps of 20°. In this way, the pattern could be moved back and forth at 18 different angles, thus allowing the measurement of directional tuning functions. Recordings were made with glass microelectrodes filled with KCl (1 M), so recordings were usually intracellular but some extracellular spikes were measured. Recordings lasted for 5–30 min with most at the lower end of this range. The unreliability of the recording period forced me to use short stimulus tests to obtain the maximum number of repetitions. Motion responses were measured in 1–5 s periods and responses were always the average spike rates in the first second. To reduce the possible influence of adaptation on the results (Ibbotson & Goodman 1990), the rest period between motion phases was always twice the length of the stimulus period.

3. RESULTS

Recordings were obtained from 96 motion-sensitive neurons in the descending nerve cords of 85 bees. The neurons fell into four categories, 47 cells being direction-selective optomotor neurons of the type previously reported (Goodman *et al*. 1987; Ibbotson & Goodman 1990; Ibbotson 1991*a*, 1992). The number of recordings was biased toward these cells because they are the largest diameter neurons in the nerve cord. Twelve of the 96 neurons showed clear direction-selective responses, but their velocity tuning was quite different from the optomotor neurons. The responses of these 12 neurons form the basis of the new discoveries presented here. The neurons will be referred to as velocity-tuned (VT) cells to distinguish them from the optomotor neurons. Twenty-four neurons were multimodal, showing responses to flashing lights, puffs of air and moving images, but the preferred stimulus could not be identified. Thirteen cells responded selectively to the movement of small black objects against white backgrounds but did not respond consistently to the grating stimulus. The last two cell types will not be described here.

The VT neurons were rarely encountered, making detailed analysis of their response properties problematic. It was difficult to hold the cells for longer than 5 minutes, possibly indicating relatively small axon diameters. One recording from a VT neuron was stable enough to complete all the directional and velocity tests (using 1 s motion periods and 2 s rest periods between motion) and then to record responses to longer motion periods of 5 s. Peristimulus time histograms from this neuron to motion in its preferred direction at 70 deg s^{-1} (figure 1*a*) and 1000 deg s^{-1} (figure 1*b*) are shown. The cell produced a large response soon after motion onset but the response rapidly declined to a level well below the initial firing rate within a few seconds. The initial response is clearly far larger for the 1000 deg s^{-1} pattern, but the response magnitudes are quite similar for both image speeds at the end of the 5 s period. It would appear that adaptation has an important function in these neurons during prolonged motion stimulation.

VT neurons were direction selective, i.e. motion in one, preferred, direction produced an increase in firing rate while motion in the opposite, antipreferred, direction generated inhibition of the spontaneous activity (figure 1*c–f*). Motion perpendicular to the preferred–antipreferred axis generated no change in firing rate. The VT neurons could be divided into three types based on their directional tuning functions. All directional tuning will be described for cells in the left half of the descending nerve cord and will be presented as the animal would see it. For example, for frontal stimulation, 0° (or 360°) indicates horizontal motion to the right, 180° indicates horizontal motion to the left and 270° downward motion (figure 1*c*,*e*,*f*). For lateral stimulation, 0° is back-to-front image motion and 180° is front-to-back motion (figure 1*d*). When stimulated in the frontal visual field, six neurons were maximally sensitive to horizontal motion to the animal's left (figure 1*c*), two were maximally sensitive to motion downwards and to the left (225°; figure 1*e*) and four cells were sensitive to downward motion (figure 1*f*). Two of the horizontal sensitive neurons were tested with the stimulus in the lateral visual field (left eye) and were maximally responsive to horizontal motion from front to back (figure 1*d*). The directional tuning functions of the horizontal neurons had a mean half-width of 105° (six cells), while the downward-sensitive neurons tended to have narrower tuning functions (mean half-widths = 65°, six cells).

The velocity tuning of the VT cells is shown for six of the neurons (figure 2). These cells were chosen because they were stimulated with the widest range of velocities and stimulus patterns. In general, the responses increase in size with increases in stimulus speed, although some velocity tuning functions are quite flat across the whole velocity range (figure 2*b*). Most importantly, the relationship between response size and image speed is similar for the stripe widths between 11° and 76°. Although there is some variation between the response magnitudes at certain velocities for the different patterns, it appears that a sevenfold change in the spatial period of the pattern does not greatly change the shape of the velocity tuning. There was some dependence on the spatial period of the pattern, e.g. results in figure 2*b* show that the 19° pattern produces larger responses than the 11° and 76° patterns for the whole range of image velocities tested. The results in figure 2*b*,*c* show that the 11° grating tended to produce smaller responses than the patterns with larger spatial periods. The responses shown in figure 2*c–e* show larger responses to the 19° pattern than to the 76° pattern at low velocities, but similar responses at high velocities.

The graphs in figure 2 show that the responses generally increase with increasing image velocity but the beginnings of response plateaux start to appear at the highest velocities for some cells (i.e. figure 2*b–e*). As there are no clear peak responses, it is difficult to say categorically whether the neurons have a preferred image velocity. The responses for three of the VT neurons (the ones on

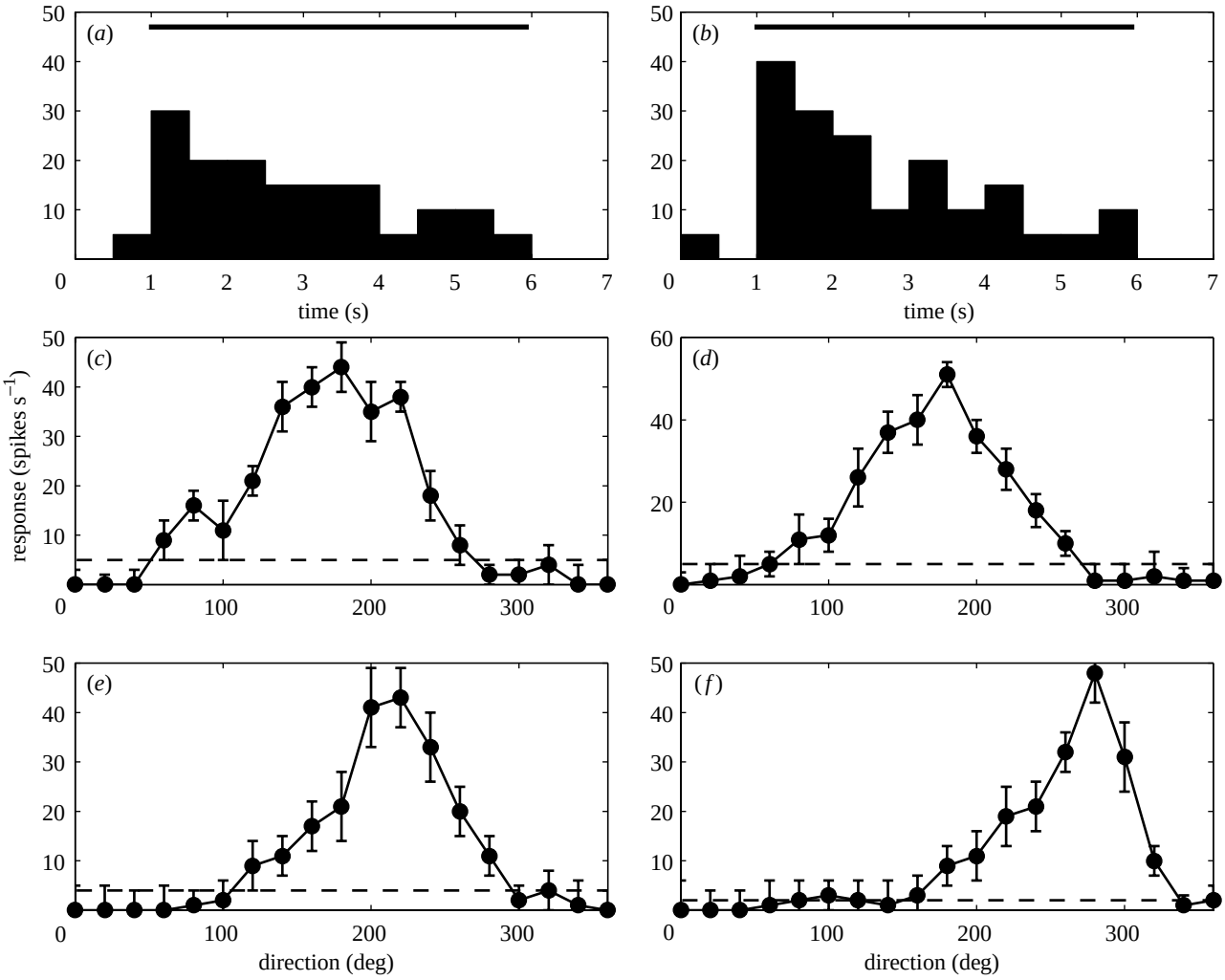

Figure 1. Peristimulus time histograms from a VT neuron stimulated with grating motion in the preferred direction at 70 deg s^{-1} (*a*) and 1000 deg s^{-1} (*b*) (bin widths: 500 ms). The horizontal bars show the motion periods. (*c*,*d*) The directional response functions for frontal and lateral stimulation for one VT neuron (*c*, frontal; *d*, lateral). (*e*,*f*) Directional response functions for frontal stimulation for two other VT neurons. The dashed horizontal lines represent the mean spontaneous activities of the neurons. Bars are standard deviations (three repetitions). All stimuli had spatial periods of 19°. The image velocity used for the directional plots was 300 deg s^{-1}.

the left of figure 2) are re-plotted in figure 3 as functions of temporal frequency. From these plots it is clear that responses of equal size occur at widely separate temporal frequencies when using the different patterns. For example, in figure 3*b* equal response magnitudes are produced for the 11° pattern at temporal frequencies an order of magnitude higher (70 Hz) than for the 76° pattern (8 Hz). This strongly suggests that temporal frequency is not the governing factor that controls response magnitude. Hence the neurons are defined as VT cells.

For comparison, the velocity tuning of two representative optomotor neurons is presented, one sensitive to leftward (figure 4*a*,*b*) and the other to downward motion (figure 4*c*,*d*). These neurons were tested with the same square-wave gratings and show quite clear differences in their velocity-tuning properties when compared with the VT cells. Both neurons are maximally sensitive to motion at different velocities for each of the patterns used (11–38°: figure 4*a*,*c*). However, when the data were plotted as a function of the temporal frequency of the gratings, the peak responses occurred consistently at values close to 10 Hz for all of the patterns used (figure 4*b*,*d*). Moreover, the roll-off in response occurred at the same frequencies for the three patterns. Therefore, the neurons are temporal frequency tuned, rather than velocity tuned.

The stimuli consisted of high-contrast square-wave gratings. Fourier analysis of a square-wave grating reveals sinusoidal spatial frequency (1/spatial period) components at the fundamental frequency (*F*) and at odd harmonic frequencies of the fundamental (3*F*, 5*F*, etc.). Therefore, a square-wave grating with a 38° period ($F = 1/38 = 0.026$ cycles deg^{-1}) will contain sinusoidal frequency components of 0.078, 0.13 and 0.182 cycles deg^{-1}, etc. The contrast in the harmonics is given by the contrast of the fundamental component (*C*) divided by the order of the harmonic. If the grating is moved at a temporal frequency of 3.3 Hz, the third-order harmonic will move at 10 Hz and will have a contrast of *C*/3. Consequently, a temporal frequency-dependent neuron optimally tuned to 10 Hz will actually respond strongly to stimulation using a high-contrast square-wave grating moving at 3.3 Hz.

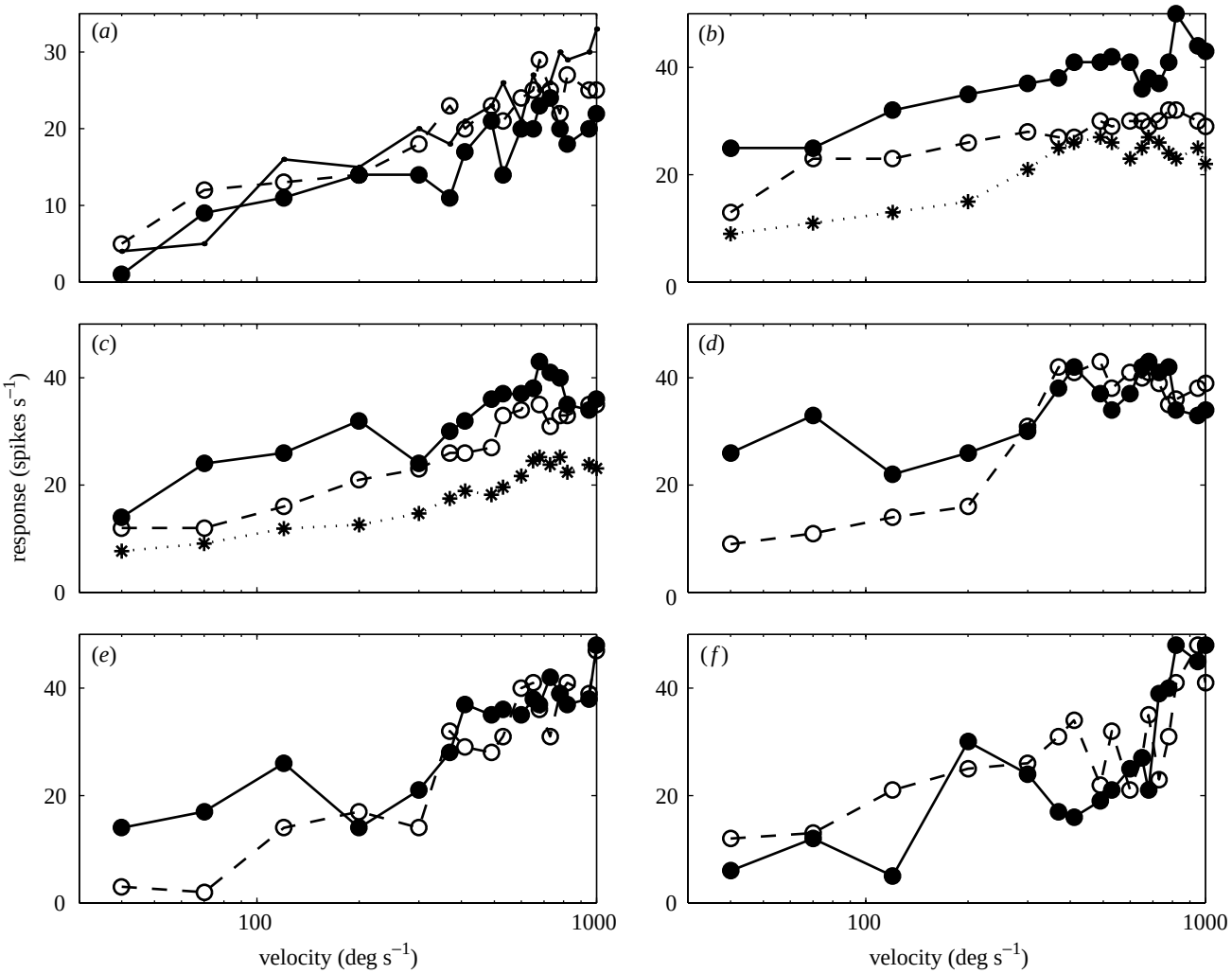

Figure 2. Velocity response functions for six VT neurons. The different symbols represent different spatial periods: stars (11°); filled circles (19°); dots (38°); and open circles (76°). Points are the means of three repetitions. (*a*) Left/down; (*b*, *c*) left; (*d–f*) down.

When using square-wave gratings, we might expect to see quite broad tuning functions where the temporal frequencies below the peak tuning are artificially high. However, for frequencies above the peak tuning (10 Hz), the harmonics will have little influence. When the fundamental spatial frequency component is moving at the peak temporal frequency, the 3*F* harmonic will move at 30 Hz. Consequently, the influence of the harmonic will be low because it is beyond the frequency that generates large responses (figure 4). The optomotor neurons produced responses for the 38° grating that were quite large at frequencies below 10 Hz. At frequencies above the peak response, the spike rates rolled off quite rapidly. In many ways, the high frequency roll-off was a better indicator of the temporal frequency dependency of the optomotor cells because it was very consistent between grating patterns. We must also consider that the gratings in the periphery of the visual field would have lower spatial periods than the stated values due to the convex curvature of the stimulus and the bee's eyes. Despite this, the optomotor neurons showed clear temporal frequency dependence while the responses of the VT neurons were better correlated with the velocity of the patterns.

4. DISCUSSION

Without doubt, the most commonly studied motion-sensitive neurons in the insect visual system are the direction-selective cells that make up the optomotor control system. Extensive studies in a wide range of insects have shown that these neurons are temporal frequency dependent (e.g. Ibbotson 1991*a* (bees); Hausen 1984 (flies)), as are the behavioural optomotor responses they drive (Kunze 1961 (bees); Götz 1964; Hausen & Wehrhahn 1989 (flies)). For example, in bees, optomotor yaw torque responses peak at 8–10 Hz and cut off at *ca.* 100 Hz for a range of spatial frequencies (Kunze 1961). As shown in figure 4, bee optomotor neurons generate maximal responses at frequencies close to 10 Hz at all spatial frequencies (also see Ibbotson & Goodman 1990; Ibbotson 1991*a*). Consequently, there is a good match between the tuning of the identified cells and the behavioural output. VT neuron responses either steadily increase in spike rate as the image velocity increases up to the maximum velocity tested or they reach a plateau response at relatively high image speeds. The spatial period of the gratings did not greatly affect the shape of

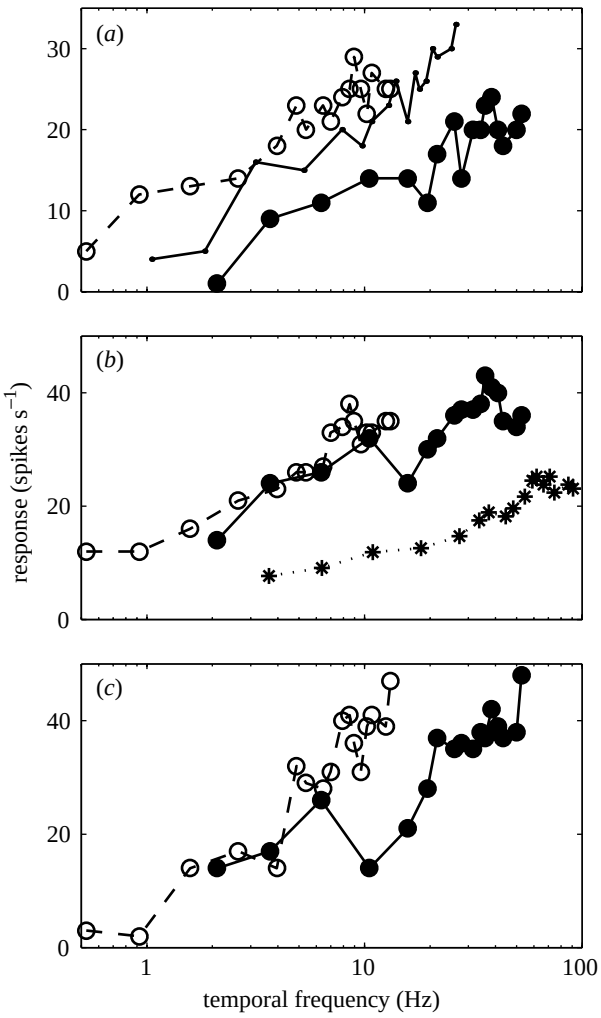

Figure 3. The responses shown in figure 2*a*,*c*,*e* are re-plotted as functions of temporal frequency in (*a*), (*b*) and (*c*), respectively. Symbols are the same as in figure 2.

the response functions in relation to image velocity, but it did influence the absolute magnitudes of the responses (e.g. the 11° pattern in figure 2*b*,*c*). Presumably, even a VT system will have some limit on response magnitude imposed by the spatial configuration of the inputs. The similarities in the shapes of the velocity tuning functions with stimuli containing a very wide range of spatial frequencies (due to harmonics) provides evidence for a VT system. This conclusion is reinforced when the results are compared with those of the optomotor neurons, which clearly showed temporal tuning characteristics when using the same patterns. We can only speculate on what happens to the VT neuron responses at velocities greater than 1000 deg s^{-1}. Ultimately, the responses of the neurons will be limited by the flicker frequency beyond which movement is not perceived, which is 200 Hz in bees (Srinivasan & Lehrer 1984). What is very clear is that the temporal operating ranges of the VT cells are very different to those of the optomotor neurons. Optomotor neuron responses roll off significantly for temporal frequencies higher than 10 Hz, with only residual responses at frequencies above 70 Hz. The VT neurons, on the other hand, respond strongly at temporal frequencies of up to 91 Hz.

The present work records, so far as I know, the first time that VT neurons have been reported in the bee. Moreover, both optomotor and VT neurons were observed using the same stimuli. Only limited evidence has previously been presented showing neurons that are velocity tuned in insects. For example, extracellular recordings from lobula units in the locust revealed cells that increased their firing rate gradually with increasing velocity up to values of 460 deg s^{-1} (Kien 1975). This relationship was the same at spatial periods of 13°, 19° and 31°. Similarly, the firing rates of descending neurons in the dragonfly were shown to increase with increasing velocity up to values of 150 deg s^{-1} with square-wave gratings ranging in spatial period between 8 and 22° (Olberg 1981). At velocities above 150 deg s^{-1}, the response levels remained constant up to velocities of 500 deg s^{-1}, except for the 8° grating, which showed a decrease in firing rate for velocities above 150 deg s^{-1}. Horridge & Marcelja (1992) recorded responses from motion-sensitive neurons in flies, locusts, dragonflies and butterflies that showed a fairly steady increase in firing rate for sinusoidal gratings with 11.5° and 23° spatial periods up to velocities of 400 deg s^{-1}. They contrasted the responses of these neurons with the responses of optomotor neurons. As with the results in the bee, the operating ranges of the optomotor neurons were at far lower temporal frequencies.

What makes the results presented here particularly interesting is that honeybees have been comprehensively tested for a range of visual behaviours in free flight. Therefore, it is possible to compare VT responses to the behavioural output. Behavioural experiments have suggested the existence of at least two functionally distinct movement-sensitive pathways in bees: one tuned to temporal frequency, mediating optomotor responses, and another tuned to velocity, subserving range computation and control of flight speed (Srinivasan & Lehrer 1984; Srinivasan *et al*. 1993, 1996; Srinivasan & Zhang 1997). The VT neurons are sensitive to horizontal front-to-back motion over the lateral eye regions or to downward and leftward motion in the frontal visual field. During forward flight there would be a component of downward motion on the frontal lower parts of the eyes and a back-to-front motion over the equatorial regions of the lateral parts of both eyes. It would be interesting to record the responses of VT neurons to simultaneous stimulation of the lateral regions of both eyes. If they were involved in monitoring forward flight speed we would expect them to be optimally sensitive to simultaneous front-to-back motion over the lateral equatorial regions of the eyes and possibly to downward motion in the lower regions of the frontal visual field. A descending neuron sensitive to back-to-front motion over the lateral regions of the eyes has been identified in the bee (Ibbotson 1991*b*); however, its velocity tuning was not measured in detail. That cell was quite broadly tuned for direction, as are the horizontal sensitive neurons presented here. It is possible that the anatomically identified cell generated some of the responses recorded in the present experiments.

Without more detailed knowledge of the directional tuning of the VT neurons, it is difficult to speculate on their precise role in monitoring optic flow fields. However, useful discussion arises from comparing the velocity tuning of the VT cells with the image velocities

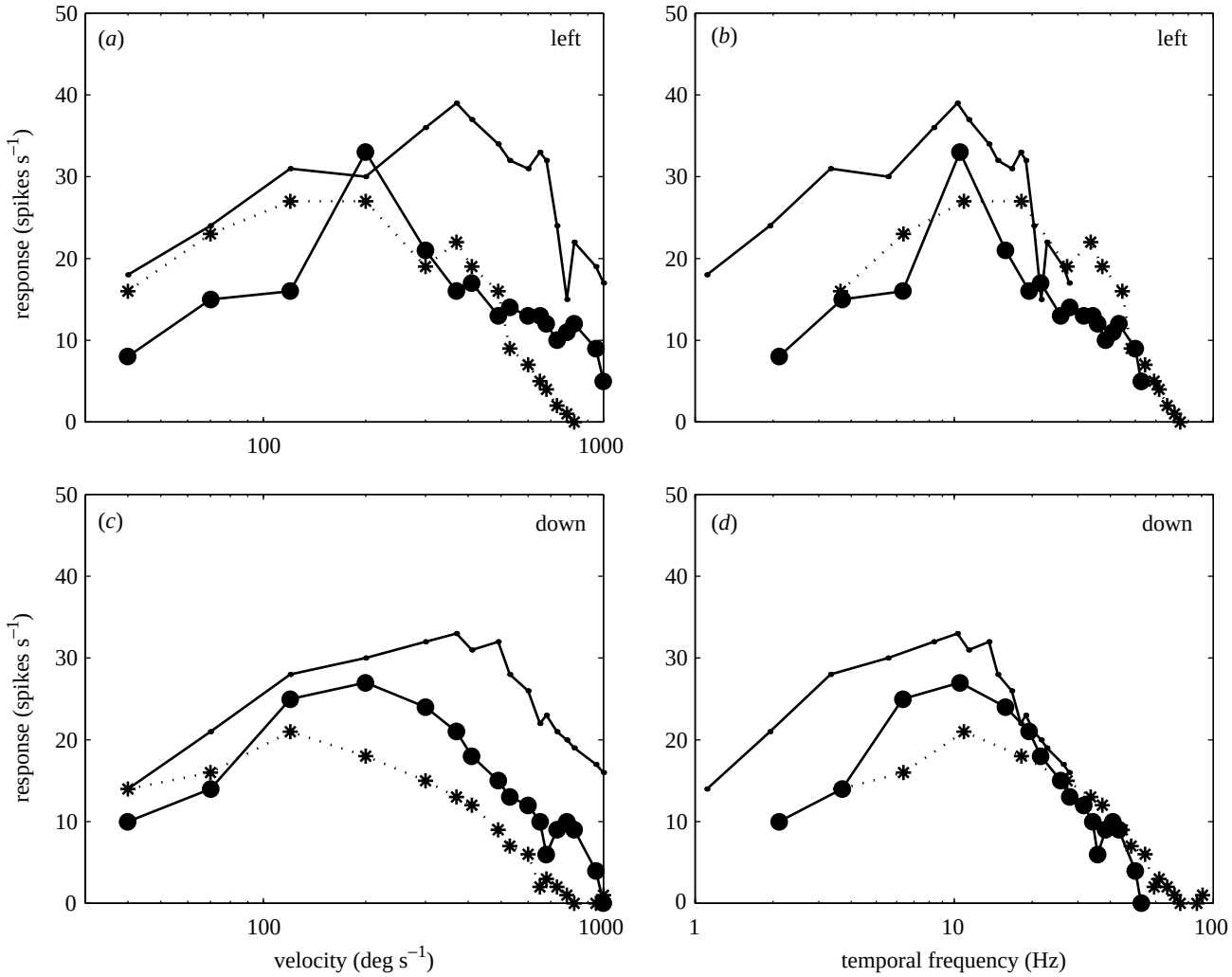

Figure 4. Responses are plotted for two optomotor neurons as functions of image velocity (*a*,*c*) and temporal frequency (*b*,*d*). The cell in the upper plots was sensitive to leftward motion and the cell in the lower plots to downward motion. The neurons show peak responses, which correspond to temporal frequencies close to 10 Hz (*b*,*d*). The peaks occur at different image velocities for each pattern (*a*,*c*). Line and symbol conventions are as in figure 2. Points are the means of three repetitions.

generated on the eyes of freely flying bees. The image velocities generated on the surface of the eyes as bees fly through tapered tunnels have been measured in the range from 90 to 250 deg s^{-1} (Srinivasan *et al*. 1996). The spatial periods experienced in the tunnels ranged from 17 to 45°. During landing, bees decrease their forward speed steadily as their altitude decreases such that forward speed is approximately proportional to altitude. This indicates that the bees are holding the angular velocity of the image of the surface constant as they approach the surface. The angular velocities occurring on the eyes during landing ranged between 400 and 600 deg s^{-1} (Srinivasan *et al*. 1996). The speed ranges outlined above fit within the velocity tuning ranges of the VT neurons. Importantly, most VT neurons would not have reached their plateau responses at 400–600 deg s^{-1} (figure 2), so the cells could measure changes in velocity without saturating. As the VT neurons are velocity tuned and they respond over the appropriate velocity range, it is certainly possible that they are involved in flight speed control in bees. Ultimately, any VT signals generated by the visual system have to be transferred to the thoracic motor centres for flight speed to be altered. It makes sense to look for such neurons in the descending nerve cord. A fuller understanding of the flight speed control mechanism will come from anatomically identifying the VT neurons and stimulating them with more sophisticated stimuli that better simulate the complex optic flow fields generated during locomotion, i.e. see Krapp (2000), Frost & Wylie (2000) and Duffy & Wurtz (1995).

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