Fig. 2. Time course of the flow velocity as measured in a water tunnel behind a swimming fish via laser-Doppler anemometry (frequency resolution 200 Hz) at the outer edge of the vortex street (above) and at the height of the vortex cores (below). Large turbulences occur when passing through the boundary layer, swimming speed ca. 0.47 m s$^{-1}$, site of measurement ca. 3 cm behind the caudal fin (scale: vertical 5 cm s$^{-1}$, horizontal 100 ms)

overcome surface drag as estimated for rigid, streamlined bodies. Efficiency, defined as the ratio of propulsive power to the sum of propulsive power and the power wasted in the fluid, amounts to about 70 %. The undulatory pump supports the generation of the potential vortices surrounding the vortex cores which entail about 80 % of the total energy found in the wake [4].

In conclusion, subundulatory swimming fish generate during steady locomotion a flow pattern in the wake which was predicted for highly efficient swimmers like tunas. The velocities in this wake are rather high and their special distribution represents a signal which might entail information on size and speed of a swimming fish. In order to maintain high efficiency a considerable evolutionary pressure must exist inducing fish to generate a flow pattern with low kinetic energies, i.e., a chain of vortex rings. Flow preformation achieved by the pumping action of the undulating body helps to distribute the sites of work along the axis of the fish.

1. Lighthill, M. J.: Mathematical biofluid dynamics. Philadelphia: Soc. Industr. Appl. Math. 1975
2. Hess, F., Videler, J. J.: J. Exp. Biol. 109, 229 (1984)
3. Webb, P. W.: Bull. Fish. Res. Board. Can. 190, 1 (1975)
4. Rayner, J. M. V.: J. Fluid. Mech. 91, 697 (1979)
5. Spedding, G. R.: J. Exp. Biol. 125, 287 (1986)
6. Rosen, W. M.: US Naval Ord. Test. Stat. Techn. Prod. 2298 (1959)
7. Hertel, H.: Biologie und Technik. Mainz: Krauskopf 1963
8. Blickhan, R., Krick, C., Nachtigall, W.: Verh. Dtsch. Zool. Ges. 83, 630 (1989)
9. Bleckmann, H., Breithaupt, T., Blickhan, R., Tautz, J.: J. Comp. Physiol. A 168, 749 (1991)
10. Chopra, M. G., Kambe, T.: J. Fluid Mech. 79, 49 (1976)

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# Is There a Separate Control System Mediating a "Centering Response" in Honeybees?

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In a series of recently published experiments [1, 2] Srinivasan and colleagues found that trained bees flying freely through a tunnel covered with vertical grating patterns tend to fly in the middle of the tunnel. Two observations are particularly interesting. (1) If the patterns on both walls are stationary but have different spatial wavelengths, the distribution of the bees is still centered around the midline of the tunnel. (2) When the pattern on one of the walls is moving opposite to the bees' direction of flight and, thus, the apparent image velocity increases on this side, the average location of the flight trajectories is shifted towards the stationary wall. The authors interpret this behavior as a "centering response" mediated by a separate control system different from all optomotor control systems analyzed so far. They conclude that their results demonstrate "directly and unequivocally, that flying bees estimate the distances of surfaces in terms of the apparent motion of their images" (p. 519 in [2]). Moreover, from the finding that on the bees' average flight paths the temporal frequencies perceived by both eyes may differ by almost one order of magnitude, while the apparent velocities are, on average, fairly similar, the underlying motion detection system is concluded to measure the angular speed of the patterns independently of their texture and, therefore, to be much different from the well-studied compensatory optomotor system sensitive to rotation around the vertical body axis.

Free flight studies on motion information processing in insects are most valuable and badly needed to set the context for the many behavioral studies done on tethered flying animals, but are difficult to perform. However, the conclusions drawn by Srinivasan and colleagues may not be as unequivocal as they believe. A possible flaw in their conclusions lies in the fact that the output of the optomotor system of honeybees is implicitly treated as a monotonically increasing function of temporal frequency which is unambiguously determined by this stimulus parameter. If this assumption were valid, the optomotor system would indeed never acquire a state of equilibrium in the tunnel as soon as the tex-

tures of the walls differ to some extent. Because the temporal frequency does not change with the distance from the walls, a balance of temporal frequencies could not be achieved by compensatory lateral shifts of the animal. Unless the control system mediating optomotor turning responses is switched off or overruled by other control systems, it would then be hardly conceivable that bees endowed with such an optomotor system would ever reach the end of the tunnel.

Fortunately, however, the optomotor system does not behave in this way. Behavioral as well as electrophysiological experiments on insects (for review, see [3, 4]) including honeybees [5 – 7] reveal that the optomotor response increases with increasing temporal frequency only within a certain range, reaches an optimum, and then decreases again (Fig. 1 A). This experimental finding is not surprising, given the fact that no conceivable motion-detecting system can distinguish zero from infinite speed. These considerations show that the same response level may be attained at considerably differ-

ent temporal frequencies. Consequently, the optomotor system may be balanced, even if the temporal frequencies perceived by the two eyes differ to a large extent [8]. Hence, the possibility that the bee relies to a large extent on its optomotor system in finding stable flight trajectories in a three-dimensional world and, thus, also in the tunnel employed by Srinivasan and colleagues [1, 2] should not be too rashly discarded on the erroneous assumption that the optomotor system balances the temporal frequencies on both eyes.

Indeed, a comparison of the stimulus parameters used in the study of Srinivasan and colleagues with published data on the optomotor system of honeybees [5 – 7] indicates that the output of the optomotor system on both sides of the brain may not differ much. For instance, the temporal frequencies at which optimal responses of the optomotor system are achieved lie in the range 8 – 10 Hz [5 – 7]. Figure 9 in [2] reveals that when the patterns on both walls of the tunnel are stationary and the pattern periods differ by a factor of 4, the temporal frequencies perceived

by one of the eyes is smaller and the temporal frequency perceived by the other eye is larger than the optimal temporal frequency. When the pattern periods differ only by a factor of 2, there are also many cases where the temporal frequencies on both eyes are smaller than the optimal temporal frequency. However, in these cases the temporal frequencies induced by the bees' translatory movements do not differ much (i.e., only by a factor of 2). In either case the output of the corresponding optomotor neurons on both sides of the visual system is expected to be rather similar and thus the optomotor system roughly belanced allowing for a stable flight path through the length of the tunnel.

The optomotor balance has been found to be disturbed when one of the patterns starts moving, for instance, in the opposite direction to the flight path of the bee [2]. In this case the apparent temporal frequencies elicited by the moving wall plus the bee's own motion increase. By comparing Fig. 9 and Fig. 10 in [2] with the experimental data on the bee's optomotor system [5 – 7], it is suggested that the resulting temporal frequencies perceived by the eye are, on average, less optimal than when the wall was stationary. In this case, the responses of the optomotor system on this side of the brain are expected to decrease. If the optomotor system were only dependent on temporal frequency, no stable position could be reached at any location whatsoever, since the temporal frequency does not change with the distance from the walls.

However, the optomotor response of insects is not exclusively determined by the temporal frequency of the stimulus pattern. It also strongly depends, among other parameters, on the spatial frequency content of the pattern (for review, see [3]). In the case of a periodic grating the output of the optomotor system increases with decreasing spatial frequency, reaches an optimum, and then decreases again (Fig. 1 B) and, therefore, is altered, even at a constant temporal frequency, when the spatial wavelength of the pattern changes. Taking the temporal and spatial frequency dependence of the optomotor system together, it is clear that it can attain constant response levels for an indefinite number of combinations of temporal frequencies and spatial wave-
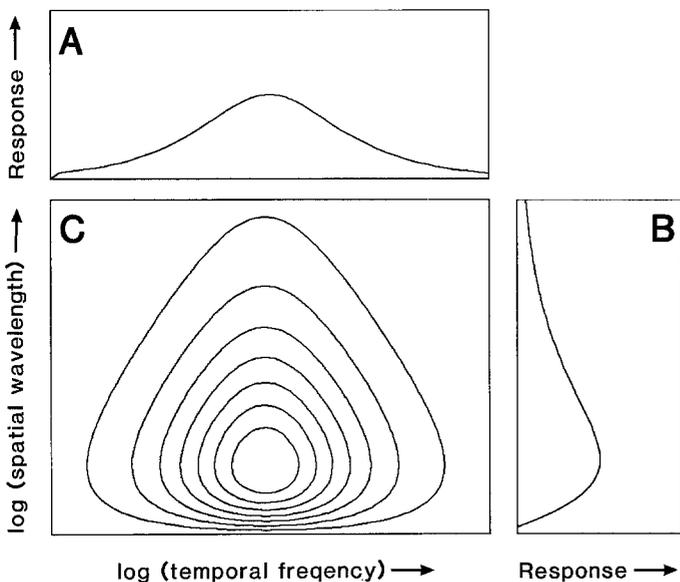


Fig. 1. Schematic illustration of the temporal frequency and spatial wavelength dependence of the insect optomotor system sensitive to rotation around the vertical body axis. A) Response amplitude as a function of the logarithm of temporal frequency. The spatial wavelength of the stimulus grating with sinusoidal brightness modulation is held constant. B) Response amplitude as a function of the logarithm of the spatial wavelength. The temporal frequency of the grating is held constant. Note orientation of axes. C) Contour plot of the optomotor response as a joint function of temporal frequency and spatial wavelength. The contour lines are iso-response lines. The inner lines represent the larger response amplitudes. Equal response amplitudes are elicited by an infinite number of combinations of spatial and temporal frequencies. As a consequence, the optomotor system on both sides of the animal may be balanced even when both eyes perceive quite different motion stimuli

lengths (Fig. 1 C). It could be this peculiar feature that allows the optomotor system, by varying the distances to the two walls of the tunnel, to return to a new state of equilibrium when one wall of the tunnel starts moving, because spatial frequency varies with lateral position. For instance, for the grating with a fundamental period of 10 cm the spatial wavelengths ranged from about 80° as perceived by the bee when flying in the center of the tunnel to 60° or 100° when it was either 9 or 3 cm from the wall. For the grating with a fundamental period of 2.5 cm the corresponding values were 24°, 16°, and 45°, respectively. Although the dependence of the bee's optomotor system on the spatial structure of stimulus patterns has not yet been adequately analyzed so far, it seems to be likely from corresponding measurements done on the fly (for review, see [3]) that the spatial wavelengths employed in the tunnel experiments are below the optimum wavelength of the motion detection system of the bee. In this case, the bee's optomotor system can reach an equilibrium only by flying on a trajectory near the stationary wall. The spatial wavelengths on this side are expected to then become somewhat less optimal, while the wavelength on the other side becomes more optimal. Thus, the optomotor system can compensate for asymmetries on both sides as they are induced by the moving grating.

These arguments suggest that the evidence put forward so far [1, 2] is not sufficient for postulating a new control system that is specifically destined to mediate a "centering response". Instead, the published data are likely to reflect the necessity of the bee to balance its optomotor system in order to allow for a straight flight path.

However, two restrictions have to be made. Both the conclusions of Srinivasan and colleagues [1, 2] as well as the interpretations given above are based on two assumptions that are not quite satisfied under the experimental conditions of the study. (1) The optomotor system has to operate in its steady state, otherwise none of the predictions made by Srinivasan et al. or proposed above are exactly valid. With flight speeds ranging between 10 and 70 cm/s [2], the time it takes the bees to pass the tunnel of 40 cm length varies between about 0.6 and 4 s. Although the dynamic properties of the optomotor system of bees have not yet been analyzed systematically, the comparison of the available data of bees [5 – 7] and flies [9] suggests that it takes at least between 1 and 2 s for the optomotor system to settle at its steady-state level. Therefore, considerable transient response components are expected to affect the behavior of the bees. However, the consequences of these components for the bees' behavior in the tunnel cannot easily by predicted. (2) All the predictions concerning the temporal and spatial frequency dependence of the optomotor system apply only to sinewave gratings. However, in most of the experiments Srinivasan and colleagues used gratings with a squarewave intensity profile. Hence, in all these experiments the bee is confronted with a mixture of spatial frequency components and, accordingly, temporal frequencies. The contribution of the higher-frequency components to the overall response can be expected to be all the more pronounced as the fundamental frequencies of the gratings used in the experiments were rather low and most likely well below the optimal spatial frequency of the optomotor system (see above). Interestingly, in the only experiment where sinewave gratings were used, Srinivasan et al. [2] report a slight but significant pattern dependence of the flight trajectory when the spatial wavelengths differed by a factor of 4. This is in ac-

cordance with predictions that can be made if the bees were governed in the tunnel by an ordinary optomotor system.

In conclusion, the tunnel experiments done by Srinivasan and colleagues [1, 2] nicely reveal the extraordinary navigating skills of freely flying honeybees and, therefore, are extremely important in understanding the visual orientation behavior of insects. Nevertheless, taking all the above arguments together, we do not believe that the published data provide conclusive evidence for a new flight control system. Although this may be difficult to do with freely flying animals, because the stimulus conditions can only be partly controlled by the experimenter, further experiments are required before a final assessment of their behavior in the tunnel experiments is possible.

1. Kirchner, W. H., Srinivasan, M. V.: Naturwissenschaften 76, 281 (1989)
2. Srinivasan, M. V., Lehrer, M., Kirchner, W. H., Zhang, S. W.: Vis. Neurosci. 6, 519 (1991)
3. Buchner, E., in: Photoreception and Vision in Invertebrates, p. 561 (Ali, M. A., ed.). New York-London: Plenum 1984
4. Borst, A., Egelhaaf, M.: Trends Neurosci. 12, 297 (1989)
5. Kunze, P.: Z. vergl. Physiol. 44, 656 (1961)
6. Ibbotson, M. R., Goodman, L. J.: J. Exp. Biol. 148, 255 (1990)
7. Ibbotson, M. R.: J. Comp. Physiol. A 168, 91 (1991)
8. Götz, K. G.: ibid. 99, 187 (1975)
9. Hausen, K.: Biol. Cybern. 46, 67 (1982); Maddess, T., Laughlin, S. B.: Proc. R. Soc. Lond. B. 225, 251 (1985); Ruyter van Steveninck, R. de, Zaagman, W. H., Mastebroek, H. A. K.: Biol. Cybern. 54, 223 (1986); Egelhaaf, M., Borst, A.: J. Opt. Soc. Am. A 6, 116 (1989); 7, 172 (1990)