VISUAL PROCESSING

Flies go with the flow

Mandyam V. Srinivasan

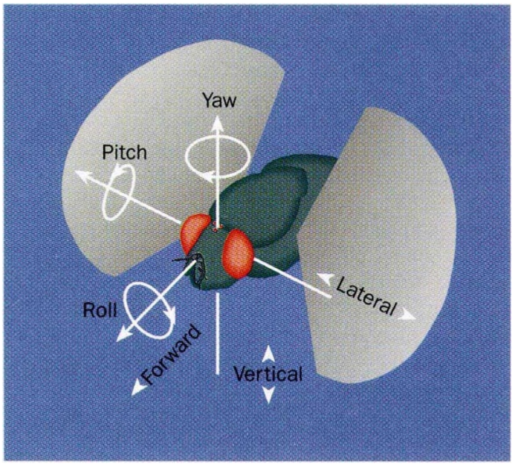
ANYONE who has watched a fly perform a flawless landing on the rim of a teacup will know that even relatively small and 'simple' nervous systems can orchestrate impressive visuomotor coordination. To accomplish such manoeuvres — or even merely to move in a straight line — a flying creature needs to be able to keep track of its own motion by monitoring the apparent motion of its surroundings as it moves. Understanding exactly how this is achieved has challenged neurobiologists for decades. The paper by Krapp and Hengstenberg[1] in this issue (page 463) sheds new light on how the pattern of image motion that is experienced by the moving eye is analysed by the nervous system of the fly (*Calliphora erythrocephala* Meig.) to deduce motion in three-dimensional space and at a given instant in time.

A flying insect can move with six degrees of freedom: it can yaw, pitch or roll, as well as translating forwards, laterally or vertically (see figure). In principle, these motions can be inferred from the patterns of image motion, or 'flow fields', that they create in the eyes. For example, yaw generates forward motion of the image in one eye, backward motion in the other, and no motion either directly overhead or directly below. Forward translation produces backward motion of the image in both eyes, and no motion in the frontal or rearward regions of the visual field. Roll causes upward motion of the image in one eye and downward motion in the other, and, again, there is no motion in the front or rear.

These patterns of image motion are thought to be detected by a handful of neurons in a region of the fly's brain known as the lobula plate[2]. These neurons have large visual fields and they are highly sensitive to motion stimuli from the eyes. Krapp and Hengstenberg have used a new technique to map the receptive fields and response properties of these neurons in a very precise fashion. Their results indicate that each neuron is exquisitely 'tuned' to sense the pattern of image flow that results from a specific type of motion of the animal.

The key feature of the new technique is the visual stimulus, which allows the experimenter to determine — precisely and rapidly — the flow field to which each neuron is tuned. The stimulus consists of a spot that moves at a constant speed in a small, circular trajectory. Typically, a neuron in the lobula plate shows a fluctuating response to such a stimulus.

The maximum sensitivity of the neuron to image motion (within the small region of the receptive field that is stimulated by the rotating spot) is determined by the difference between the largest and the smallest values of the response, measured over one cycle of rotation of the spot. The 'preferred' direction of image motion within this region is determined by the direction in which the spot is moving when the response is maximal (after appropriate correction for the delay in the response). So the local sensitivity of the neuron to image motion can be characterized by a vector whose magnitude represents sensitivity, and whose direction represents the locally preferred direction. These measurements can be repeated at different regions in the visual field by repositioning the stimulus, which is carried on a calibrated cardan arm. The final result is a group of vectors that describes the pattern of image motion to which the neuron is tuned.



R. Hengstenberg

Flight control — a flying insect can move within six degrees of freedom and, in the paper discussed here, Krapp and Hengstenberg[1] analyse the way these movements are interpreted in terms of patterns of image motion by a fly's nervous system.

Krapp and Hengstenberg[1] have used this method to investigate one class of neurons in the lobula plate, the so-called VS neurons. Until now these neurons were thought to respond simply to image motion in the vertical direction[2]. The new results show that these neurons are more specifically tuned — they respond most strongly to rotation about an axis in the horizontal plane. One subset of the VS neurons responds best to rotations about the fly's long axis (roll); another subset is stimulated by rotations about a transverse axis (pitch); and yet another responds best to rotations about an axis lying between these two. Taken together, the responses of these neurons can encode rotations about any axis in the horizontal plane.

Another neuron, Hx, is maximally silenced when the fly moves in the forward direction. Together with neurons that are tuned to other directions of translation, Hx could, in principle, encode the direction of translation in three dimensions. But further work is needed to discover and characterize all of the neurons that might be involved in evaluating self-motion.

These findings raise important questions as to the number and types of neurons that are involved in computing self-motion; precisely how information on self-motion can be encoded by the pattern of activities in such an ensemble of neurons; the minimum number of neuron types that would be necessary for this purpose; and the role of any redundancy. It would also be interesting to compare results in flying insects — many of which move with six degrees of freedom — with results in walking insects (such as ants), which are restricted to forward translation and yaw. Finally, many of these considerations could be valuable in the design of vision-based algorithms for the navigation of mobile robots.

The discovery that motion-sensitive neurons in the lobula plate of the fly are tuned to respond to specific flow fields is echoed by similar findings in vertebrates. For example, there are neurons in the nucleus rotundus of the pigeon brain[3] and in the medial superior temporal area of the monkey brain[4], that signal an approaching object by responding specifically to expanding images. The emerging principle, which was clearly foreshadowed about a decade ago[5], seems to be that the brain makes sense of the chaotic world by viewing it through sensory filters that are 'matched' to meaningful external events. ☐

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