Orientation detectors in insects

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INSECTS perform highly sophisticated visual tasks with a tiny brain. This implausible conjunction has often led people to suppose that insects analyse visual patterns in ways which avoid the need for heavy computation, and that the mechanisms involved differ sharply from those operating in mammals. But from the two papers on pages 539[1] and 541[2] of this issue it seems that, in at least one important respect, the mammalian visual cortex and the insect optic lobe operate upon visual patterns in a similar way. Insects, like mammals, extract the orientation of edges within the retinal image.

Bees readily learn to distinguish a pattern of stationary horizontal stripes from a similar pattern of vertical stripes. Srinivasan, Zhang and Rolfe[1] have asked how bees do so. One possibility is that they are blind to the spatial properties of the stimuli and that they can distinguish horizontal from vertical only because the two stripe-patterns activate different classes of motion detectors; that is, detectors of vertical motion will be stimulated best when a bee approaches or moves past horizontal stripes, whereas the signature of vertical stripes will be a discharge from detectors of horizontal motion. This possibility should be taken seriously, for a frequent assertion is that insects are better at analysing motion patterns than spatial ones. Indeed, the optic lobe contains a wealth of neurons which respond specifically to elaborate patterns of motion, such as the optic flow fields generated on a retina when an insect turns around or flies over the ground[3], but there have been disappointingly few descriptions of neurons with interesting spatial properties.

Spatial cues

Srinivasan *et al.* now show conclusively that bees do parse visual scenes for the orientation of edges by means of purely spatial cues. Their evidence is of two kinds. First, bees can discriminate stripe orientation when patterns are presented in brief, 2-millisecond exposures, and so must be virtually stationary on the retina. Second, bees that are trained to approach horizontal stripes do not come to prefer vertically moving random-dot patterns over a similar pattern moving horizontally. On the other hand, they do favour a horizontal row of dots moving horizontally over a vertical row of dots moving vertically. So movement neither substitutes for spatial information nor disrupts it.

A feature of the stimuli is that the widths of the stripes within each pattern are random and that the arrangement of stripes is changed from trial to trial. This means that the stimuli can be discriminated only by differences in their orientation and implies that insects have neural mechanisms for abstracting this parameter.

In the second paper[2], O'Carroll describes the discovery of a new class of neuron in the optic lobe of the dragonfly. These neurons resemble simple cells of the mammalian visual cortex in responding optimally to elongated bars in a specific orientation. Their orientation tuning is broad, with the response dropping to half of its maximum when the orientation changes by 90°. Although it is tempting to suggest that analogous neurons are involved in the orientation discrimination of bees, this temptation should be resisted — at least for the time being. For one thing, the neurons in the dragonfly require moving bars to activate them, whereas bees are able to recognize stationary patterns.

What is the anatomical basis of this orientation selectivity? D. O'Carroll (personal communication) suggests an answer which is reminiscent of that proposed by Sutherland[4] to account for the ability of octopuses to recognize spatial patterns. An octopus can be taught to discriminate between vertical and horizontal bars, but it is unable to learn the difference between bars at +45° and at −45°. This finding has an anatomical correlate: the dendritic fields of cells in the octopus optic lobe tend to be elliptical with their major axis oriented predominantly horizontally or vertically[5]. So it seemed plausible that these elliptical fields are stimulated best by bars oriented parallel to their long axis, and that the lack of obliquely oriented cells explained the difficulty the octopus has in distinguishing between the two diagonals. But it was hard then to perform the necessary physiological experiments to test the idea.

Oriented dendritic fields are also seen in the optic lobes of insects[6], and O'Carroll has now been able to correlate physiology and anatomy. He finds that the dendritic processes of the orientationally sensitive neurons cover an elliptical field. The major axis is parallel to the bar-orientation which elicits the greatest response, while the length of the minor axis equals the projection of the width of the visual receptive field.

What is the normal function of insect orientation detectors? One possibility is that they provide inputs for very specific visual reflexes. For instance, houseflies fixed so that they can only roll about their long axis, orient themselves to keep edges aligned vertically in their frontal visual field[7]. Under normal conditions, therefore, they may rely on plant stems and trees to remain upright. The input for such a reflex could come from a single class of broadly tuned vertical orientation detectors.

Orientation channels

A more interesting function is that performed by orientation detectors in the primate visual cortex. Here each patch of visual space is analysed by about 18 different orientation channels. This enables the cortex to encode precisely and economically the orientation of an edge within the patch. The number of orientation channels in the dragonfly optic lobe is unknown, but work by M. V. Srinivasan, S. W. Zhang and K. Witney (personal communication) implies that bees have at least three — the minimum required for coding orientation unambiguously. When bees have been trained to approach horizontal rather than vertical stripes, they prefer the horizontal pattern over a uniform grey one and they prefer a grey stimulus over vertical stripes. Bees, thus, actively approach horizontal stripes and avoid vertical ones, suggesting that there are two or more independent channels. Unlike octopuses, they can also be trained to distinguish between +45° stripes and −45° stripes[8], bringing the total to at least three.

It would be intriguing if orientation detectors play the same fundamental role in the pattern perception of mammals and of insects. Such similarities would not have surprised the great anatomist Cajal, who, overwhelmed by his first view of the insect optic lobe, wrote:

> In comparing the visual ganglia from a bee or a dragonfly with those from a fish or an amphibian one is extremely surprised. The quality of the psychic machine does not increase with the zoological hierarchy. . . . It is as if we are attempting to equate the qualities of a great wall clock with those of a miniature watch. . . [the insect's optic lobe] is a marvel of detail, delicacy and precision[9]. □

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