

Vision: Simple stereopsis

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By limiting stereopsis to measuring the distance of moving objects against a stationary background, insects can employ simple stratagems for solving the problems of stereoscopic range finding.

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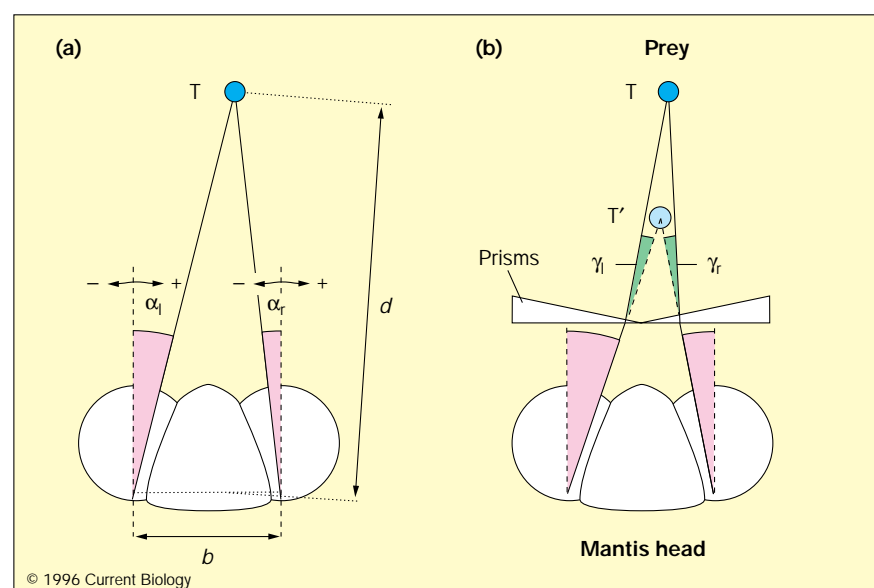
Human stereoscopic vision does not seem geared to delivering metrically accurate information about distances and shapes in three dimensions. In the absence of support from other cues, its function may be more to aid the qualitative perception of surfaces and shapes that are difficult to spot monocularly. Indeed, Julesz [1] proposed long ago that an important selection pressure in the evolution of primate stereopsis might be the need to 'break' camouflage. Similar suggestions have been made about the evolution of stereopsis in birds [2]. In certain avian families, neuroanatomical specializations for binocular vision are associated with the ability to detect and catch prey items directly from textured surfaces.

A rather different view of stereopsis, however, comes from recent studies on insects and amphibians. In these animals, stereopsis is adapted primarily to measuring the absolute

distance of prey, so ensuring that strikes are directed accurately. The evidence for this conclusion in insects comes from work on the praying mantis. Whereas mantids use stereopsis to gauge the distance of moving prey [3], they compute the distance of stationary objects in their surroundings by exploiting motion parallax [4]. The amphibian evidence is of quite a different nature. Some plethodontid salamander species are able to catch very small insects despite the latter's rapid, spring-loaded escape jumps; it has recently been shown that these species have basic neuroanatomical adaptations which enhance the speed and accuracy of their stereoscopic vision [5,6].

Probably the major difference between primates, on the one hand, and insects and amphibia, on the other, which enables the latter to compute absolute distance with relative ease is their lack of vergence eye movements (the kind we make when, for example, we look up from a book and our eyes diverge to fixate a distant object). In the absence of vergence, there is a fixed relationship between horizontal disparity and the distance of a fixated target. Stereopsis for prey capture is simpler in one other respect as well. The task is to measure the distance of a moving prey against an ignorable, stationary background. In consequence, the notorious correspondence problem, deciding which feature in the left retinal image should be matched with which feature in the right retinal image, is

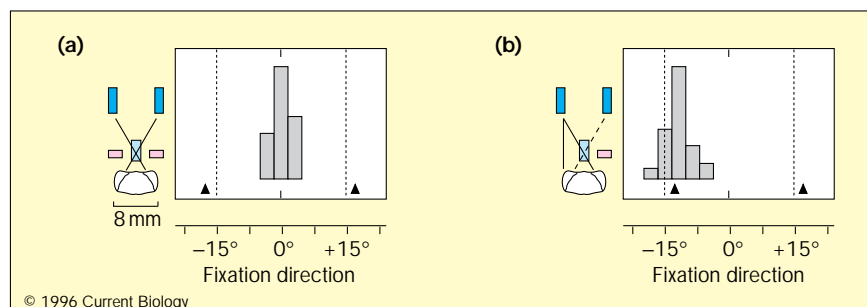
Figure 1



(a) Sketch of the head and eye of a praying mantis viewing prey (dark blue circle) at position T . α_l and α_r represent the eccentricity of the target image relative to the left and right foveas, respectively; b is the interocular separation and d is the distance of the target. The eccentricity of the target relative to a point midway between the eyes is $(\alpha_l + \alpha_r)/2$; horizontal disparity is defined as $\alpha_l - \alpha_r$. (b) The use of horizontal disparity in judging prey distance was demonstrated by having the mantis view prey through prisms which increased horizontal disparity by $\gamma_l + \gamma_r$. The mantis behaved as though a target placed at T (dark blue circle) was located at T' (pale blue circle). (Adapted from [3].)

Figure 2

Binocular fixation behaviour with occluders in different arrangements. Occluders are shown by pink horizontal bars and targets by dark blue vertical bars. The histograms show distributions of binocular viewing directions after a fixating saccade; dotted lines show angular positions of the targets and the arrowheads below the histograms give the mantid's fixation direction when there is only one target. (a) Each eye sees a different target. When there is no possibility of matching the real targets correctly, the mantid fixates midway between the two targets – it is forced to fixate a 'ghost' target (pale blue vertical bar). In this case the illusory target is closer than the normal catching



range. (b) A single occluder prevents one eye from seeing one target. The mantid fixates a

real target within catching range and does not fixate a ghost target. (Adapted from [9].)

less severe than it is for animals which are able to decode complex stationary scenes stereoscopically.

Initial models of how mantids might compute distance binocularly were beguilingly simple. Suppose, argued Rossel [7], that mantids only judge distance accurately when there is a single moving target within their visual field; horizontal disparities could then be estimated without any local binocular computations or local connections between the two optic lobes. The mantid need only measure the angular distance of the moving target-image from the left fovea in the left eye and do likewise for the right eye. Such unilateral signals from each optic lobe could then be used to control the mantid's behaviour: the average of the two signals would specify the command needed to fixate the target, and their difference would signal the target's proximity (Fig. 1).

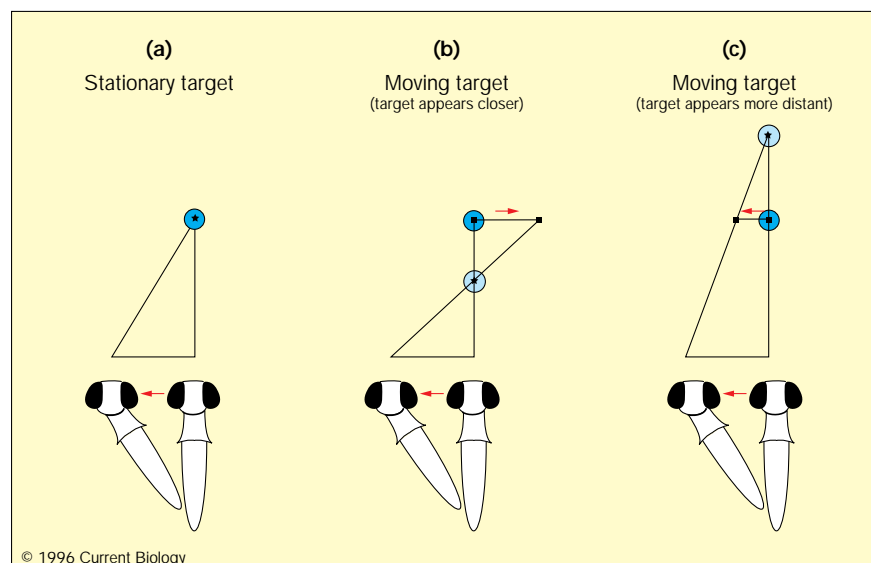
More recent findings by Rossel and colleagues, however, have shown mantids to be more subtle [8,9]. Two behavioural studies gave results which cannot be accounted for by the original model, and suggest that mantids may in fact measure disparities locally. The first of these explored the effect of using prisms to introduce vertical disparities between single targets viewed by the left and right eyes [8]. The vertical disparities did not influence the mantid's estimate of target distance, suggesting that mantids manage to separate the horizontal and vertical components of disparity. As larger vertical disparities were imposed, however, the strike frequency dropped, until with 15° of vertical disparity, mantids still fixated the mean vertical position of the targets but would no longer strike at them at all. One interpretation of this result is that large vertical disparities prevent the measurement of horizontal disparities, because the vertically disparate images on the two retinæ no longer fall within the receptive fields of local detectors of horizontal disparity.

In a new paper, Rossel [9] describes how mantids can pick out one prey when there are two moving within the visual

field. Mantids were shown two projected prey targets which moved synchronously up and down within the visual field. In such a configuration, images in the two eyes can be paired in two different ways, one of which is correct and corresponds to real objects in the world and one of which is false and generates 'ghost' targets (Fig. 2). Measurements were made of the mantids' direction of gaze after fixation. In all the experiments, the mantids tended to fixate one of the real targets rather than a ghost target; they also tended to pick out targets that fell within the normal range of catching distances in preference to targets that were either too near or too far.

To show that mantids preferred matches between images in the left and right eyes that corresponded to targets within the catching range, occluders were arranged to obscure one or both eyes' view of one target. When two occluders forced a mantid to view a different real target with each eye, its head turned to fixate a point midway between the targets corresponding to the only possible binocular pairing (Fig. 2a); the pairing in Figure 2a specifies a target that is too close to be reached with the large forelegs with which mantids strike at prey. However, when a single occluder was positioned to allow the possibility of a real match within the catching distance or a false match outside it, the mantid consistently fixated the real target and the unmatched image had no influence on the distribution of fixation positions (Fig. 2b). This ability to pick from several possible binocular pairings the one which is at the right distance is most easily explained by supposing that mantids measure horizontal disparities locally and select targets according to their disparity value.

On the face of it, this finding suggests that the mantid might be fooled into aiming incorrectly when there are two distant targets which are sufficiently close together that the ghost target due to false matches lies within the catching range. However, for an interesting reason, this configuration does not elicit an erroneous strike at the ghost. A normal prey in the catching range subtends about

Figure 3

An experiment demonstrating that insects use motion parallax for measuring the distance of stationary objects. An insect moves its head from side to side in a behaviour known as peering. If the target is stationary, range is judged correctly. However, when the target is moved in the opposite direction to the peer, image motion is exaggerated and range is underestimated. When the target is moved in the same direction, image motion is reduced and range is overestimated. The true target range is shown by a dark blue circle, the apparent target range by a light blue circle. (Adapted from [14].)

20° and mantids treat two targets that lie closer together than 20° as a single fused object. Consequently, the mantid will be unable to resolve the two distant targets and so will not strike at ghosts. This is an advantageous adaptation, as a false strike might scare away not one but two potential prey [9].

Prey capture is a ballistic movement, so measurements of horizontal disparity must be translated accurately into striking distance. Astonishingly, mantids calibrate their stereoscopic system without any binocular experience. In order to reach their adult size, mantids pass through a maximum of ten nymphal stages. At each stage the eye enlarges by the addition of ommatidia at the medial margin of the eye, so that regions of eye which acted initially as the fovea come to serve lateral vision. If one eye is masked to deprive it of light throughout this lengthy and elaborate developmental process, the mantid remains competent to perform accurate, binocularly driven strikes at prey immediately the eye cover is removed [10].

Mantids use quite different means to judge the distance of stationary targets such as plant stems. Before jumping onto a nearby stem, they perform a side-to-side slow scanning movement known as peering. This causes the target to move over the retina at a velocity that is determined by both the distance of the target and the animals' own peering speed. Poteser and Kral [4] have recently adapted a technique, first used by Wallace [11] on locusts, to prove that peering does indeed generate useful distance information.

When an experimenter moves the target in the opposite direction to the mantid's movement, so exaggerating image

motion, the insect jumps short. When the target is moved in the same direction, the mantid jumps too far (Fig. 3). Side-to-side peering is rarely seen during prey capture, and indeed mantids with their bodies fixed strike accurately at approaching prey at a distance that is determined entirely by binocular disparity [7]. This task segregation suggests strongly that stereopsis in mantids is adapted specifically for estimating the distance of moving targets such as prey. In stationary scenes, when images in the two eyes cannot be easily matched, insects employ motion cues instead.

Amphibians also use binocular cues to judge the distance of their prey. However, unlike mantids which rely completely upon stereopsis, some anurans use a variety of cues. The grass frog, *Rana pipiens*, for instance, feeds mostly on terrestrial prey, such as snails moving slowly over the ground. When prey is restricted to the ground plane, its retinal elevation within the frog's lower visual field can provide a rough measure of distance: objects imaged low in the visual field are seen as close, and ones higher as further away. This crude estimate is refined in part through stereoscopic information [12].

Roth and colleagues [5,6] have shown that some plethodontid salamanders have developed an unusual binocular neural pathway and an extra-fast protrudable tongue, which can be fully extended in 10 milliseconds or less [13]. The standard binocular pathway described in frogs and toads has always seemed a little makeshift as a substrate for stereopsis. The eyes project directly to the contralateral optic tectum, the visual area most concerned in prey localization. However, each eye communicates with its ipsilateral tectum by a rather circuitous route *via* the

contralateral optic tectum and the nucleus isthmi. These ipsilateral and contralateral projections are in spatial register, so that in each tectum there is an ordered representation of the binocular portion of the visual field. The design fault of this organization is that the indirect ipsilateral projection introduces a temporal delay of about 30 milliseconds between signals reaching the tectum from the two eyes. This delay may cause errors in localizing small and fast moving targets.

Some plethodontids are sit-and-wait predators and tend to catch tiny prey, like springtails, by rapidly extending their tongue. The prey are caught at very close range, so that retinal image speeds may be high. To cope with these problems, there is an additional ipsilateral pathway, so that each eye projects directly to both tecta, ensuring that signals from the two eyes arrive synchronously with minimal delay. Clinching evidence that this system is adapted to the binocular assessment of prey distance comes from recordings by Wiggers *et al.* [6] of binocular neurons in the optic tecta two different-sized species. The mean tongue extension of the larger species is about 20 mm and that of the smaller species is about 13 mm. In both species, tectal neurons have been recorded which have binocular receptive fields. When the binocular field of a neuron is mapped into object space, the distance at which the two fields coincide usually lies within reach of the salamander's tongue, and the recorded population of binocular cells in each species covers nicely the whole range of possible catching distances.

On the face of it the mantid and salamander stereoscopic systems perform very similar jobs. As the two systems become better understood, it will be fascinating to learn how convergent the stereoscopic mechanisms of these different animals turn out to be.

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