70. Humphreys, T., *Zool. Sci.*, 1987, **4**, 1129.
71. Burglin, T. R. *et al.*, *Nature*, 1991, **351**, 703.
72. Kenyon, C. and Wang, B., *Science*, 1991, **253**, 516–517.
73. Walldorf, U., Fleig, R. and Gehring, W. J., *Proc. Natl. Acad. Sci. USA*, 1989, **86**, 9971–9975.
74. Wright, C. V. E., Cho, K. W. Y., Hardwicke, J., Collins, R. H. and De Robertis, E. M., *Cell*, 1989, **59**, 81–93.
75. Nohno, T. *et al.*, *Cell*, 1991, **64**, 1197–1205.
76. Gehring, W. J. and Hiromi, Y., *Annu. Rev. Genet.*, 1986, **20**, 147–173.
77. Scott, M. P., Tamkum, J. W. and Hartzell, G. W., *Biochem. Biophys. Acta*, 1989, **989**, 25–48.
78. Graham, A., Papalopolu, N. and Krumlauf, R., *Cell*, 1989, **57**, 367–378.
79. Wilkinson, D. G., Bhatt, S., Cook, M., Boncinelli, E. and Krumlauf, R., *Nature*, 1989, **341**, 405–409.
80. Simeone, A. *et al.*, *Nature*, 1990, **346**, 763–766.
81. Lewis, E. B., *Am. Naturalist*, 1954, **88**, 225–239.
82. Lewis, E. B., *Am. Naturalist*, 1955, **89**, 73–89.
83. Bender, W., Weiffenbach, B., Karch, F. and Peifer, M., *Cold Spring Harbor Symp. Quant. Biol.*, 1985, **1**, 173–180.
84. Nickol, J. M. and Felsenfeld, G., *Proc. Natl. Acad. Sci. USA*, 1988, **58**, 2548–2552.
85. Choi, O. R. B. and Engel, J. D., *Cell*, 1988, **55**, 17–26.
86. Chisaka, O. and Capecchi, M. R., *Nature*, 1991, **350**, 473–479.
87. Balling, R., Mutter, G., Gruss, P. and Kessel, M., *Cell*, 1989, **58**, 337–347.
88. kessel, M., Balling, R. and Gruss, P., *Cell*, 1990, **61**, 301–308.
89. Blatt, C., Aberdam, D., Schwartz, R. and Sachs, L., *EMBO J.*, 1988, **7**, 4283–4290.
90. Kongsuwan, K., Allen, J. and Adams, J. M., *Nucleic Acids Res.*, 1989, **17**, 1881–1892.
91. Blatt, C. and Sachs, L., *Biochem. Biophys. Res. Commun.*, 1988, **156**, 1265–1270.

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Even insects experience visual illusions

Mandyam V. Srinivasan

Although the compound eyes of insects appear very different from our own eyes, research is beginning to suggest that insects experience many of the illusions that we do, and that their visual systems may process information in ways akin to ours.

It is difficult not to be intrigued by the tricks that our eyes and brain sometimes play on our perceptions. Certain visual illusions are so powerful that they cry out for an explanation. Indeed, some of the better-known illusions (reviewed, for example, by Gregory[1] and Goldstein[2]) have attracted nearly as many explanations as explainers!

Illusions are more than mere curiosities. They can illuminate the ways in which information is processed by the visual pathways. Recent years have witnessed mounting evidence that certain illusions are experienced not only by humans, but also by creatures such as insects, which possess relatively simple visual systems. This article describes some illusory percepts that seem to be common to man and insect, and discusses the implications of their universality.

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The 'waterfall' illusion

Many of us would have experienced that, upon staring at the water cascading down a waterfall for about a minute and then looking at the surrounding landscape, the stationary landscape appears to move distinctly *upwards* for a few seconds[2]. This illusory percept of movement in the opposite direction can also be elicited in a contemporary urban setting by watching lines of text being scrolled on a computer screen. Curiously, insects behave as though they experience this illusion as well, and experiments with them reveal a possible neurophysiological explanation.

The perception of movement by a fly can be monitored by measuring its response to a moving, striped pattern: the insect tends to turn in the same direction as the pattern[3]. This 'optomotor response' is a visual reflex which helps the insect stabilize its orientation relative to its surroundings. For example, when a pattern moves steadily to the left, as in Figure 1 *a*, it evokes a turning response to the left (Figure 1 *b*). However, when the pattern ceases to move, the fly turns briefly to the right (Figure 1 *b*), suggesting a transient perception of movement in the opposite direction.

How does this false perception come about? The answer may lie in the dynamic characteristics of the responses of directionally-selective movement-detecting neurons in the fly's optic lobe, which are believed to mediate the optomotor response[4]. The responses evoked by leftward pattern motion in two such neurons are shown in Figures 1 *c,d*. Neuron A, which responds selectively to leftward motion, produces a strong response, as shown in Figure 1 *c*. Immediately after the motion has stopped, however, the activity of this 'fatigued' neuron drops briefly to a level lower than its normal, spontaneous value. Neuron B prefers motion to the right; leftward motion inhibits its activity to a level below the spontaneous value. Immediately after the motion has stopped, however, the firing rate of this 'suppressed' neuron rises briefly to a level above the spontaneous rate. The waterfall illusion is readily explained if we assume that the perception of motion, and the behavioural response to it, are determined by a comparison of the instantaneous activities of pairs of neurons, such as A and B, with opposing preferred directions. When the pattern is in motion toward the left, the firing rate of A would be higher than that of B, resulting in a correct perception of motion along the preferred direction of A. Immediately after the pattern stops, however, the instantaneous firing rate of B would be temporarily higher than that of A, resulting in a brief, erroneous perception of motion in the opposite direction, i.e. in the preferred direction of B.

Thus, the fly appears to experience the same illusion of movement as we do, and the perception of this illusion can be accounted for in terms of the responses of movement-sensitive neurons in the optic lobe. Although similar neurophysiological explanations have been advanced for the illusion in vertebrates[5], the fly has allowed us, perhaps for the first time, to relate behaviour to physiology in the same organism, and thus to bridge the gap between the perception of motion and the neural mechanisms that mediate it.

The Benham illusion

When discs bearing black-and-white patterns as shown in Figure 2 rotate counterclockwise at a speed of 5–10 rps, most human observers perceive a yellow hue in pattern L, and a blue hue in pattern R, although each pattern is composed solely of black-and-white segments. Clockwise rotation induces a blue hue in pattern L and a yellow hue in pattern B. This phenomenon, termed the Benham illusion, is believed to be caused by interactions between the mechanisms by which the visual system processes signals spectrally, spatially and temporally[6–8]. The precise nature of the interactions remains to be discovered, and is a subject of some debate[9,10]. Interestingly, however, honeybees, which are known to possess colour vision, behave as though they experience an illusion of a similar nature[11].

This was demonstrated by training freely-flying honeybees to discriminate between patterns R and L rotating counterclockwise continuously at 30 rps, and presented in a horizontal plane immediately beneath the surface of a glass-topped table. One group of bees was trained to prefer to land above pattern R by associating this stimulus with a food reward consisting of a drop of sugar water. The bees learned this task well; after having received 30 rewards, they showed a significantly greater proportion of landings above the rotating R stimulus when their relative preference for the two stimuli was tested with the reward removed[11]. When these trained bees were offered a choice between two structureless, stationary disks, one coloured ultraviolet and the other green, they showed a significant preference for the ultraviolet disk. However, another group of bees, trained by associating pattern L with a reward, showed a significant preference for the green disk in subsequent tests of colour preference. This experiment demonstrates clearly that the bees perceive different hues in the two rotating patterns, and suggests that L induces a 'warmer' hue than R. The exact hues perceived by the bees remain to be discovered.

Experiments carried out by rotating the patterns at various speeds suggest that the bees experience the illusory colours most vividly at a rotational speed of 30 rps. This optimum speed is commensurate with what one might expect on the following grounds. Considering that humans experience the illusion best at speeds of 5–10 rps[6,7,12] and that the temporal resolving power of the honeybee's visual system, measured in terms of flicker-fusion frequency, is approximately four times that of man[13–16], one may *a priori* expect the illusion to be strongest in the range 20–40 rps for the honeybee, on the assumption that the mechanisms responsible for the illusion are similar in man and honeybee, but faster in the insect by a factor of four.

Illusory contours

If four dark circles, each divested of one quadrant are arranged as shown in one of the patterns in Figure 3 *c*, the human observer perceives an illusory white rectangle. That is, the cut-out corners in the four circles induce illusory connecting edges between them. It has

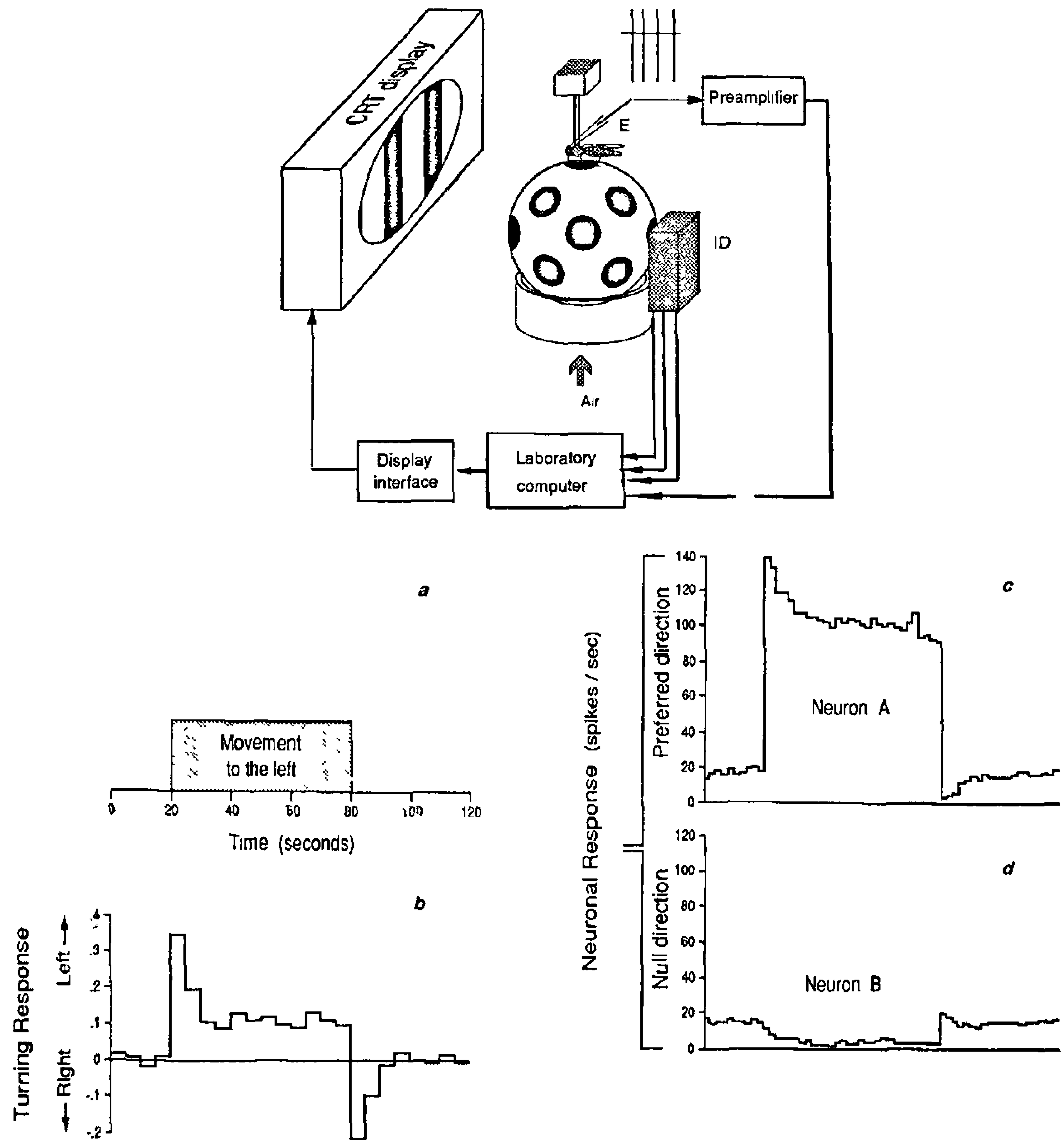

Figure 1. ***Experiment suggesting that flies experience the waterfall illusion.*** The visual stimulus is a pattern of vertically-oriented stripes, displayed on a CRT by a laboratory computer. The pattern remains stationary for an initial period of 20 sec, then moves to the left in the horizontal direction at a velocity of 25 deg per sec for 60 sec and, finally, remains stationary for a period of 40 sec before it disappears and is replaced by a uniform field of the same mean luminance. This stimulus cycle is repeated several times and the evoked responses (behavioural as well as neural) are monitored and ensemble-averaged by the computer. The tethered fly walks on a ping-pong ball supported by a gentle stream of air. As the fly walks, it rotates the ball. Rotations about the vertical axis and about a horizontal axis perpendicular to the animal's long axis are monitored by sensing optically the motion of a black-and-white pattern painted on the ball, using an array of infrared reflective-surface detectors (ID) interfaced to the computer. The turning response of the walking fly is measured in 5-sec bins as the ratio of the angles turned by the ball about the vertical and horizontal axes. This ratio is a measure of the curvature of the path that the fly would have taken, had it been walking freely. In another series of experiments, the responses elicited by the same moving stimulus in individual, large-field movement-detecting neurons in the visual pathway are measured by inserting a microelectrode (E) into the lobula plate, amplifying the electrical signal and feeding it to the computer. The neuronal response is measured as the instantaneous frequency of spikes (action potentials). The 120-sec stimulus cycle is divided into 2 sec bins and the average spike frequency associated with each bin is computed by dividing the number of spikes in the bin by the duration of the bin. ***a***, Stimulus cycle; ***b***, Turning response evoked in a single animal (averaged over 50 stimulus cycles); ***c***, Response evoked by the stimulus in a neuron (neuron A) which prefers leftward motion (averaged over 5 stimulus cycles); ***d***, Response evoked by the stimulus in a neuron (neuron B) which prefers rightward motion (averaged over 5 stimulus cycles). Movement of the pattern toward the left (between 20 sec and 80 sec (***a***)) causes the fly to turn in the same direction. When the pattern ceases to move (at 80 sec, (***a***)), the fly turns briefly in the *opposite* direction, as if it experienced a transient, oppositely directed movement. This illusion can be 'explained' at the neurophysiological level in terms of the responses of a pair of directionally-selective movement-detecting neurons in the fly's brain, one sensitive to leftward movement (neuron A) and the other to rightward movement (neuron B), as described in the text.

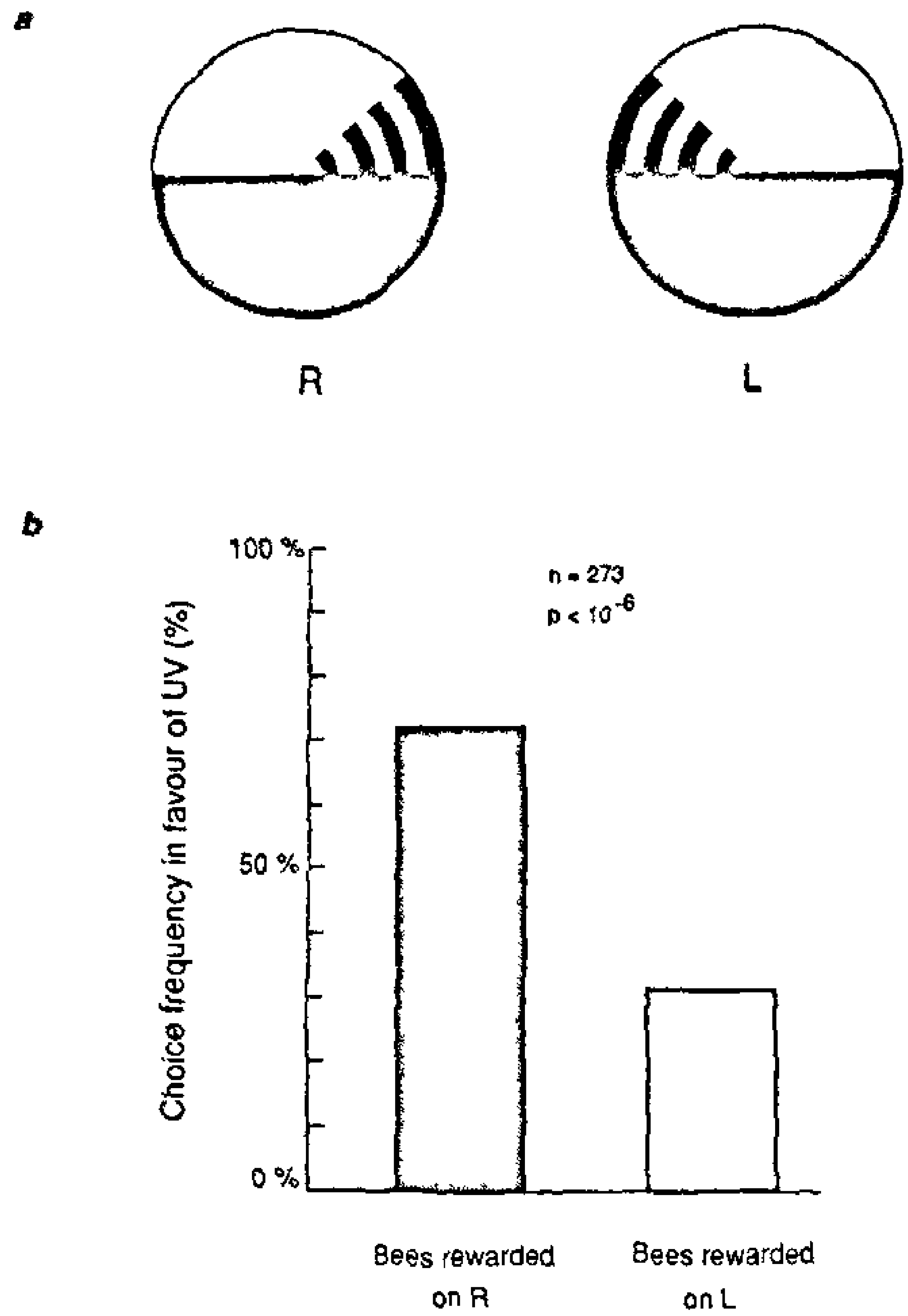

Figure 2. ***The Benham Illusion.*** ***a***, In most human observers, pattern R induces a blue hue when it is rotated counterclockwise and L induces a yellow hue when it is rotated in the same direction. Clockwise rotation of the patterns induces the opposite colour sensations. ***b***, Behavioural training experiments indicate that honeybees also experience illusory colours whilst viewing these rotating patterns. Bees are trained to distinguish between R and L rotating counterclockwise, and subsequently their colour preferences are tested by offering them two colours, ultraviolet (UV) and green. Bees that have been rewarded on R prefer the UV (shaded bar), whilst those that have been rewarded on L prefer green (light bar). This demonstrates that the bees perceive a longer-wavelength hue in L than in R. *n* is the total number of landings analysed in the two training experiments and *p* is the confidence level in a Chi-squared test for a statistically significant difference in the choice preferences exhibited by the two groups of bees.

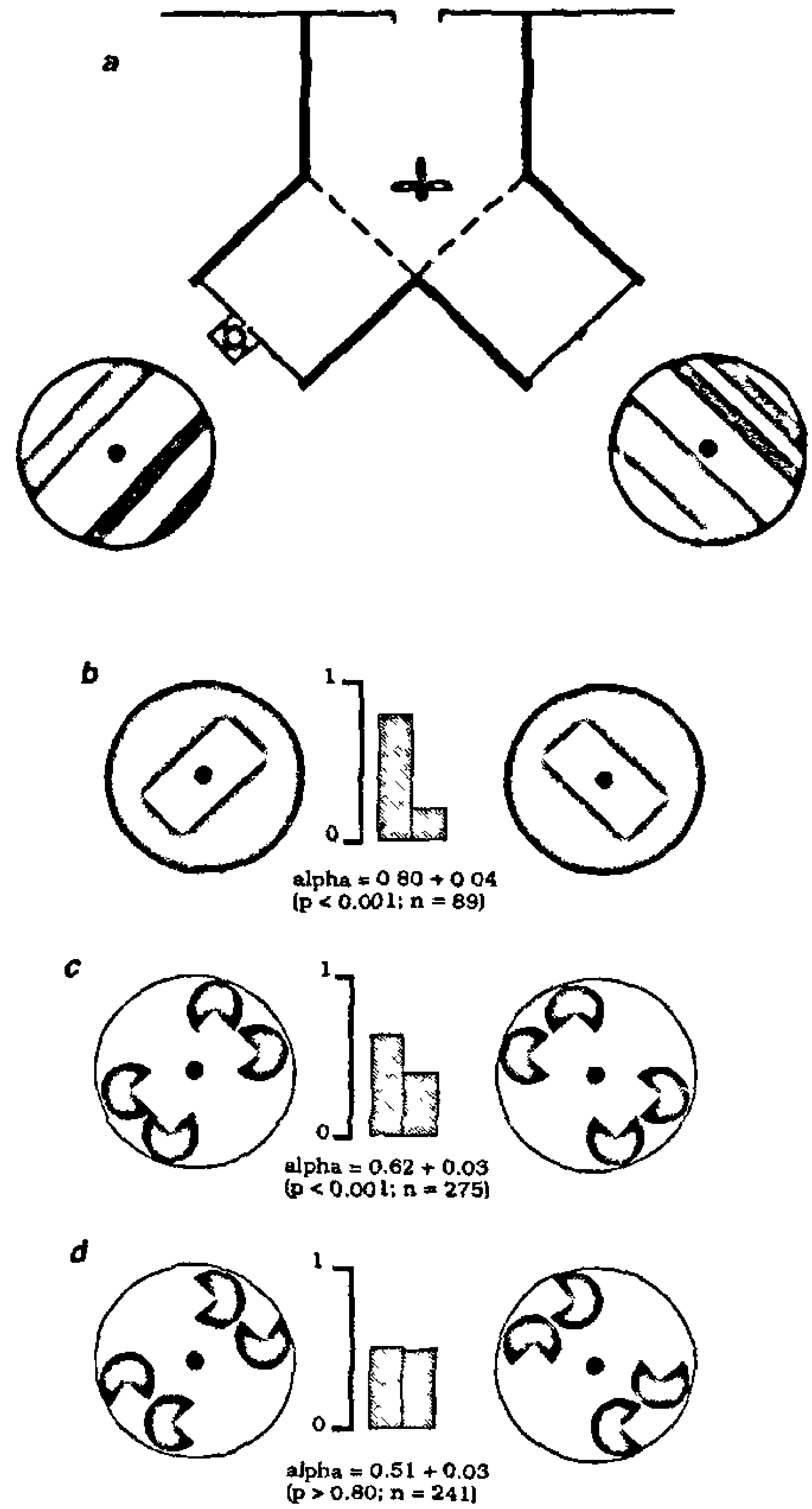

Figure 3. ***Perception of illusory contours by insects.*** ***a***, Bees can be trained in a Y-maze to distinguish between striped patterns of two different orientations (+45 deg and −45 deg) by associating one of the orientations (+45 deg) with a reward of sugar water, offered in the Box B. Bees trained in this way are then tested with other pairs of patt , such as in (***b***), (***c***) and (***d***). In (***b***), the bees prefer the rec' .ngle oriented at +45 deg, in (***c***), they prefer the illusory rectangle oriented at +45 deg, in (***d***), where the illusion no longer exists for humans, the bees show no preference for either pattern. The histograms depict the relative choice frequencies for the two patterns offered in each test, measured by scoring a large number of decisions (*n*). In each case, *alpha* refers to the choice frequency in favour of the pattern shown on the left, and *p* is the confidence level in a Chi-squared test for statistically significant departure from random choice.

been suggested that these phantom contours represent an attempt by the brain to arrive at a sensible interpretation of the figure[17] (in this case, four dark circles on a white background, with a white envelope placed over the dark circles). It has also been suggested that illusory contours aid in the perception and recognition of objects that are partially occluded by other objects in the foreground[18]. Is this phenomenon restricted to creatures with higher cognitive capacities?

Recent experiments in our laboratory suggest that illusory contours are perceived even by bees. Honeybees can be trained to discriminate between differently-oriented striped patterns, as in Figure 3*a*, and to use orientation as a parameter to distinguish between other patterns that they have never previously encountered. Thus, bees which have been trained to distinguish between the two patterns in Figure 3*a*, by associating a reward with the pattern on the left, show a distinct preference for a pattern with the same dominant orientation when offered the two white rectangles shown in Figure 3*b*. .Interestingly, when the same trained bees are shown two figures which, in humans, evoke the perception of rectangles (Figure 3*c*), the bees show a statistically significant preference for the illusory rectangle with the same dominant orientation. Our illusory percept of the rectangles is broken when the cutout circles at the corners are rotated by 90 degrees, as in Figure 3*d*; curiously, the trained bees then show no preference for either figure!

Could this imply that bees perceive illusory contours in the same way that we do? It is tempting to suggest that this is indeed the case. While such a conjecture is difficult to prove conclusively, it has recently been bolstered by further behavioural experiments in which bees were tested on a variety of phantom contours, and by the discovery that certain neurons in the insect optic lobe respond to such contours[19].

The Mueller-Lyer illusion

To most of us, the distance between the tips of a pair of arrowheads appears longer when the arrowheads point inwards, rather than outwards (compare the arrowheads in the upper and lower halves of Figure 4*a*). What is the reason for this illusion? Several explanations have been hypothesized, too numerous to discuss individually here. The interested reader is referred to the reviews in refs. 1, 2, 20, 21. One interesting explanation attempts to relate the perceptual phenomenon to the pattern of movements that the eyes execute whilst viewing such figures. By monitoring the eye movements, Yarbus[22] showed that the regions in which the gaze tended to linger longest were the areas *within* the arrowheads. That is, whilst viewing an arrowhead, the gaze tends to be directed toward a location which corresponds roughly to the centre of gravity of the arrowhead. Therefore, if one assumes that the distances between the arrowheads are perceived in terms of the distances between the regions of visual fixation associated with each of them, then it follows that the perceptual distance between the inward-pointing arrowheads will be greater than that between the outward-pointing arrowheads. Note that an explanation of this kind does not crucially require the presence of eye movements or visual fixation. A simple variant which postulates movements of a 'focus of attention', rather than eye movements *per se*, would produce the same results[23].

A few years ago, Geiger and Poggio[24] examined the visual fixation behaviour of flies as they viewed the Mueller-Lyer figures. A tethered, flying fly viewed the figures attached to the inside of a vertical drum in a specially-constructed 'flight simulator'. In this apparatus the yaw torque exerted by the fly was measured by a transducer, whose output controlled the rotation of the drum (the visual 'panorama'). A yaw torque in the clockwise direction caused the drum to rotate counterclockwise and vice versa. This approximated the visual consequences of the fly's turning manoeuvers in free flight—at least with respect to rotations about the vertical axis. In this setup, therefore, the fly could view any region of the figure by exerting the appropriate yaw torque. Curiously, the visual fixation patterns of the flies were very similar to those of humans: the distance between regions of high fixation probability (Figure 4*b*) was greater when the arrowheads pointed inward than when they pointed outward! Could it be, then, that flies are deceived by the Muller-Lyer figures just as we are? The above experiment does not allow us to answer this question with an unequivocal 'yes', but it does permit a speculative 'maybe'! At the very least, these data show

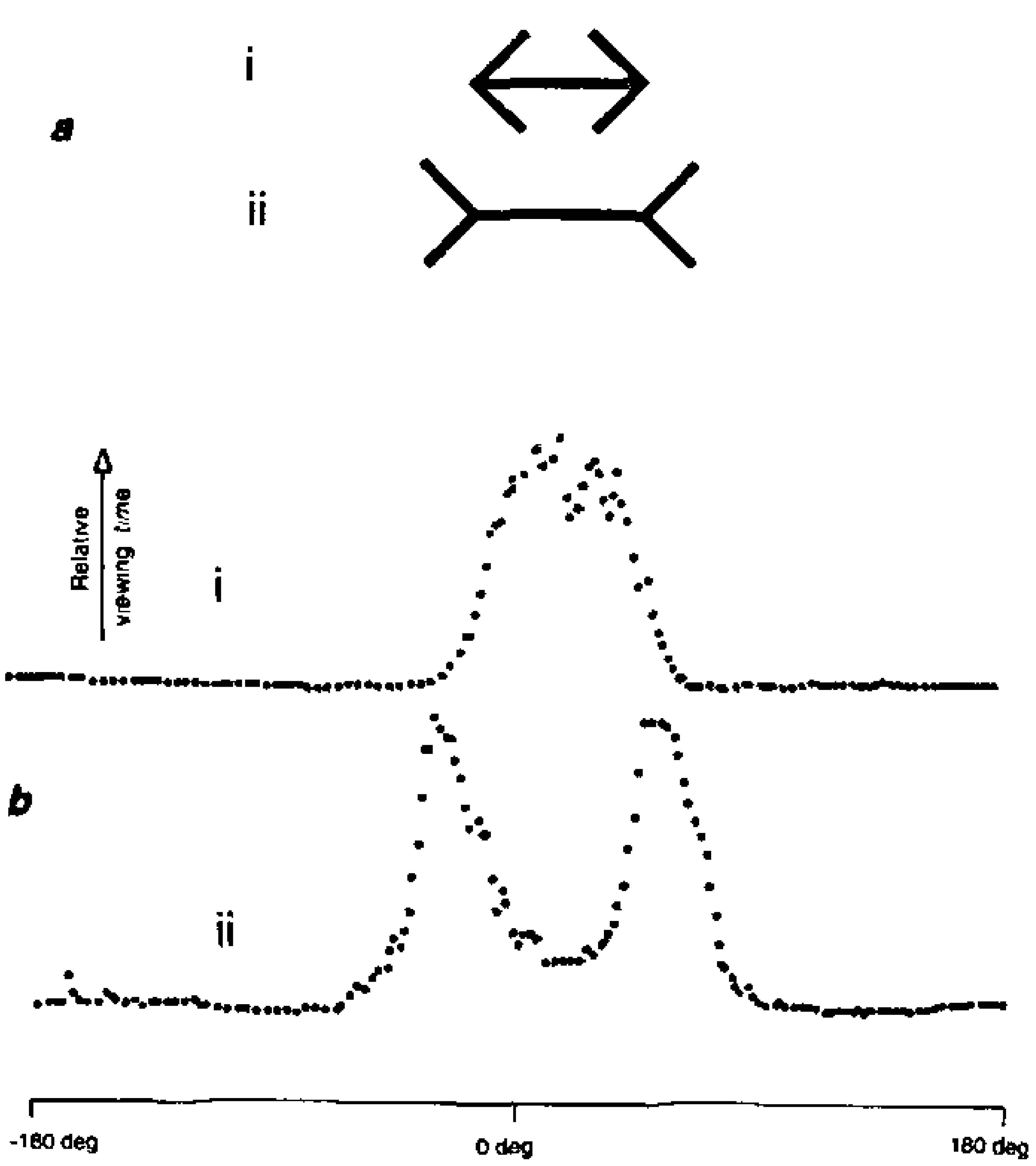

Figure 4. ***The Mueller-Lyer illusion.*** The horizontal segments in the two figures shown in (*a*) are of the same length, although the one associated with the outward-pointing arrowheads (i) appears to be shorter. A tethered, flying fly is suspended in the centre of a vertical drum and coupled to a flight simulator as described in the text. When each of the illusory figures is displayed, in turn, on the inside of the drum, the fly exhibits the fixation probability distributions shown in (*b*). These histograms show the relative amounts of time the fly spends viewing each 1-deg sector of the drum. For each figure, the regions of longest fixation tend to be near the centre of gravity of each arrowhead. Humans display a very similar pattern of fixations whilst viewing the same figures If we assume that the distances between the tips of the arrowheads are perceived in terms of the distances between the regions of high fixation density associated with the arrowheads, then the perceptual illusion in humans is readily explained The finding that the Mueller-Lyer figures elicit similar patterns of fixation in humans and flies suggests (but does not prove) that flies experience the illusion just as we do.

that flies and humans exhibit the same pattern of visual fixations whilst viewing the illusory figures.

Discussion

Traditionally, a number of visual illusions experienced by humans have been explained by invoking cognitive percepts. For example, the illusory rectangles in Figure 3*b* can be accounted for by saying that our brain decides that the most likely interpretation is that of a white paper envelope partially occluding four dark circles. An alternative interpretation, of four black circles, each divested of one quadrant and arranged in precisely the right positions and orientations (or of a white rectangle viewed through four circular holes) is exceedingly unlikely. These alternative explanations are based on the assumption that perception depends upon prior knowledge of objects in the visual world and of situations that are likely to be encountered[25]. Such an interpretation loses its plausibility, however, when one finds that the illusion is experienced even by insects, which, presumably, have no cognizance of rectangular objects or of the geometrical 'rules' of occlusion. A more likely explanation, then, is that the phantom contours are generated by 'low-level' mechanisms which operate to 'bridge' gaps between collinear contours. Such mechanisms would help 'complete' the contours of partially occluded objects without requiring the participation of any higher-level processes, such as those involved in recognition. This notion is corroborated by the discovery of neurons, in fairly early stages of processing in the visual cortex of the monkey, which respond to the 'illusory' edges that we perceive[26].

Cognitive explanations have also been advanced for the Mueller-Lyer illusion[1,2,20,21]. One widely known explanation proposes that the mind's eye interprets each pair of arrowheads as a perspective view of, say, a rectangular sheet of folded paper. The inward-pointing arrowheads depict a view of the concave side of the paper, with the folding crease (the imaginary line connecting the tips of the arrowheads) farthest from the viewer. The outward-pointing arrowheads, on the other hand, depict a view of the convex side of the paper, with the folding crease nearest to the eye. Since the two creases subtend the same visual angle—despite the fact that the first crease is farther away from the eye—the mind's eye concludes that the first crease is actually longer than the second. Such an explanation assumes that the eye-brain system has a very good *a priori* knowledge of what to 'expect' to see in the visual world (the arrowhead pair is more likely to represent a folded, rectangular sheet of paper than an unusual two-dimensional object). It also assumes that the eye–brain system possesses a working knowledge of the rules of perspective geometry. While this could be a plausible interpretation of the illusion in humans, it is very difficult to sustain for creatures such as insects, which have limited cognitive faculties. The finding that even flies behave as though they experience the Mueller-Lyer illusion therefore argues against explanations based on interpretations of perspective projection, and favours simpler, low-level explanations based on spatial distributions of visual fixation or attention.

In conclusion, the study of illusions in insects—apart from being fascinating in its own right—is worthwhile for three reasons. Firstly, the finding that insects are deceived by certain visual stimuli in the same way that we are, suggests that similar principles of visual processing may be shared by a variety of organisms across the animal kingdom. Secondly, given that the nervous systems of insects are simpler than those of their mammalian counterparts and contain far fewer neurons (e.g. ca. 875,000 neurons in the bee brain as opposed to ca. 10,000,000,000 neurons in the human brain), it may be easier to unravel the physiological basis of some of these illusions in insects. Thirdly, wherever insects seem to experience the same illusions as humans, one must question the validity of explanations involving higher cognition or 'top-down' processing.

1. Gregory, R. L., Eye and Brain, Princeton University Press, 1990.
2. Goldstein, E. B., *Sensation and Perception*, Wadsworth, Belmont, California, 1984.
3. Reichardt, W., in *Processing of Optical Data by Organisms and by Machines* (ed. Reichardt, W.), 1969, pp. 465–493.
4. Srinivasan, M. V and Dvorak, D. R., *Vision Res.*, 1979, **19**, 1435–1437.
5. Barlow, H. B. and Hill, R. M., *Nature*, 1963, **200**, 1345–1347.
6. Campenhausen, C., *Z. vergl Physiol.*, 1968, **60**, 351–374.
7. Campenhausen, C. von, *Die Sinne des Menschen. I.* Georg Thieme Verlag, Stuttgart, 1981.
8. Zrenner, E., in *Colour Vision* (eds. Mollon, J. D. and Sharpe, L. T), Academic Press, New York, 1983.
9. Campenhausen, C. von, Hofstetter, K., Schramme, J. and Tritsch, M. F., *Vision Res.*, 1992, **32**, 913–923.
10. Lehrer, M., Wunderli, M. and Srinivasan, M. V., *J. Comp. Physiol.*, 1993, **A172**, 1–6.
11. Srinivasan, M. V., Lehrer, M. and Wehner, R., *Vision Res.*, 1987, **27**, 1285–1289.
12. Sheppard, J. J., Rand Corporation Memorandum, RM-4470-ARPA, Santa Monica, Calif.
13. Autrum, H. and Stoecker, M., *Z. Naturforsch.*, 1950, **5b**, 38–43.
14. Kelly, D. H. Flicker, in *Handbook of Sensory Physiology* (eds. Jameson, D. and Hurvich, L. M.), 1972, Springer-Verlag, vol. 7/4, pp. 273–302.
15. Srinivasan, M. V. and Lehrer, M., *J. Comp. Physiol.*, 1984, **155**, 297–312.
16. Srinivasan, M. V. and Lehrer, M., *J. Comp. Physiol.*, 1985, **157**, 579–586.
17. Kanizsa, G., in *The Perception of Illusory Contours*, (eds. Petry, S. and Meyer, G. E.), Chapter 4, 1987, pp. 40–49, Springer-Verlag, New York, Berlin.
18. Peterhans, E. and von der Heydt, R., *Trends Neurosci.*, 1991, **14**, 112–119.

19. Horridge, G. A., Zhang, S. W. and O'Carroll, D., *Philos. Trans. R. Soc. London*, 1992, **B337**, 59–64
20. Hochberg, J. E., *Perception*, Prentice-Hall Inc, Englewood Cliffs, New Jersey, 1978.
21. Kaufman, L., *Perception: The World Transformed*, Oxford University Press, New York, 1979.
22. Yarbus, A. L., *Eye Movements and Vision*, Plenum Press, New York, 1967.
23. Srinivasan, M. V., Thathachar, M. A. L. and Deekshatulu, B. L., *IEEE Trans. Syst., Man, Cybern.*, 1975, **SMC-5**, 431–437.
24. Geiger, G. and Poggio, T., *Science*, 1975, **190**, 479–480.
25. Petry, S. and Meyer, G. E. (eds), *The Perception of Illusory Contours*, Springer-Verlag, New York, Berlin, 1987.
26. von der Heydt, R., Peterhans, E. and Baumgartner, G., *Science*, 1984, **224**, 1260–1262.

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Mycobacteria and the host*

P. R. Mahadevan

Tuberculosis (TB) and leprosy, two diseases caused by a group of bacterium called Mycobacterium, have been with the Indian population for last several years. Leprosy has been viewed with great respect as a disease caused by Almighty's curse and thus not curable. This has changed significantly during 50 years and during the last 25 years concerted efforts by governmental and non-governmental agencies on survey, education, training and treatment have come to arrest the spread of the disease and contain the foci of the infection. Tuberculosis, on the other hand, has become much more serious and unlike leprosy which is not a killer even if untreated, tuberculosis kills the individual if left untreated. Such circumstances with TB will also lead to spread of the disease. We have increasing number of tuberculosis cases and it is not getting contained, in spite of the availability of effective chemotherapy, to cure the disease within six months. Treated and cured TB patients are in millions, since they were diagnosed and effectively subjected to multidrug chemotherapy. Nevertheless, debility and also mortality in untreated persons are seen in alarming numbers.

MYCOBACTERIA have been recognized as an important group, pathogenic to human, even though they also exist in non-pathogenic forms. Mycobacteria are gram-positive bacteria classified under Actinomycetales and family Mycobacteriaceae. There are several species so far identified under the genus *Mycobacterium*. A major problem faced by microbiologists in understanding mycobacteria, unlike other organisms like *Escherichia coli*, *Bacillus*, or yeast, has been lack of well-understood self-genetic manipulation and very slow growth of the organism *in vitro*. In some cases like *Mycobacterium leprae* there is no demonstrable growth *in vitro*.

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The cell wall and membrane of the mycobacteria offer the major difference with other bacteria. The molecules constituting the envelope are responsible for acid-fastness (stainability), aggregation of cells, resistance to several drugs and lytic enzymes. The cell wall has complex lipoidal constitution. Besides the common components like Pthiocerol-dimycocersate, cord factor, sulpholipid, mycolic acid, arabinogalactan, peptidoglycan, there are special components in some species. *Mycobacterium leprae* has a unique phenolic glycolipid which is an immunodiagnostic antigen in the field use now. The significance of the lipoidal envelope becomes important when it is seen that macrophages of the immune system that are able to kill other genera of bacteria are unable to do so with some mycobacteria. This is important in the pathogenesis.

Among the species of mycobacteria that have become very relevant to human are *M. tuberculosis*, *M. leprae*,