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G. A. Horridge, S-W. Zhang and D. O'Carroll

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Insect perception of illusory contours

G. A. HORRIDGE, S-W. ZHANG AND D. O'CARROLL

Centre for Visual Sciences, Research School of Biological Sciences, Australian National University, G.P.O. Box 475, Canberra A.C.T. 2601, Australia

SUMMARY

The human visual system sees an illusory contour where there is a fault line across a regular striped pattern. We demonstrate that bees respond as if they see the same illusory contour. There is also a type of neuron in the lobula of the dragonfly optic lobe which responds directionally to motion of the illusory contour as if to an edge or line. Apparently insects have a mechanism that sees illusory contours and therefore assists in the demarcation of edges and objects at places where local contrast falls to zero at an edge, or where one textured object partially obscures another. These results suggest that insect vision, although spatially crude and low in processing power, sees separate objects by similar mechanisms to our own.

1. INTRODUCTION

One of the ways that the human visual system converts a two-dimensional stationary picture into an impression of objects in a three-dimensional world is to add contours where they do not actually exist. An illusion of a contour is created. Examples are abundant at places where the contrast locally falls to zero at an edge, where texture between foreground and background is locally similar at an edge, and where one object is obscured locally by another. This is one way that the human visual system makes use of the predictable structure of the natural world to infer three-dimensions from two. We already have an indication that insects have evolved the same ability.

In an earlier paper from this laboratory, mainly upon the discrimination of the inclination of edges when the training protocol excluded the possibility of an eidetic image being established in memory, it was reported that bees in flight apparently see the aligned contours of the Kanizsa rectangle illusion (figure 1*b*). When trained on the inclination of the Kanizsa rectangle, the bees were unable to discriminate the same global pattern without the edges aligned, and they were able to discriminate the correct inclination, learned from illusory contours, when the pattern was changed but the positive and negative inclinations retained. These results 'suggest that edge detection in the bee may involve mechanisms similar to those that lead to the percept of illusory contours in humans' (van Hateren *et al.* 1990; figure 4).

We now extend the analysis to a different type of illusory contour, which in human vision has been explained by the existence of end-stopped edge or line detectors in the striate visual cortex (von der Heydt & Peterhans 1989). The postulated mechanism in the monkey is that a line of neurons sensitive to stopped ends tends to join up because they are simultaneously excited, and this line of cells excite a higher level neuron with the appropriate inclination sensitivity. So long as sufficient stopped-end neurons are excited in a line, the higher level neuron gives the impression of a contour along the line corresponding to its own orientation. The same would apply even if the higher level detector is a group of neurons or in fact many mechanisms that detect continuity of edges. In man the illusory contour also induces local brightness changes that can be measured (Dresp & Bonnet 1991).

The illusion is so clear, and the proposed mechanism so convincing in primates, that we decided to investigate whether an insect sees the same percept of an illusory contour along a line of stopped ends and whether there are appropriate neurons in the optic lobes. The results may throw some light on the question of whether an insect has a mechanism that is adapted to detect contours and make use of them in the segmentation of three-dimensional objects from a two-dimensional pattern on the retina.

2. MATERIALS AND METHODS

The honeybees live in a hive outside the laboratory. A few of them are trained to enter the apparatus shown in figure 1*a* through a hole in the laboratory window, and are individually marked. Further recruits are discouraged except to keep up the small team of research-minded bees. The bees enter the choice chamber P from which they can see a pattern presented vertically on the end wall of each of the arms of the Y. One pattern has a sugar reward that is accessible through a tube (T) at its centre: the other has no reward but a similar tube (S) frustratingly closed at its end and painted black on the inside (to be indistinguishable visually from the rewarding side). The stimuli were made in black and white on discs 240 mm diameter, as illustrated in the figures, which are scale drawings, by cutting out black paper which

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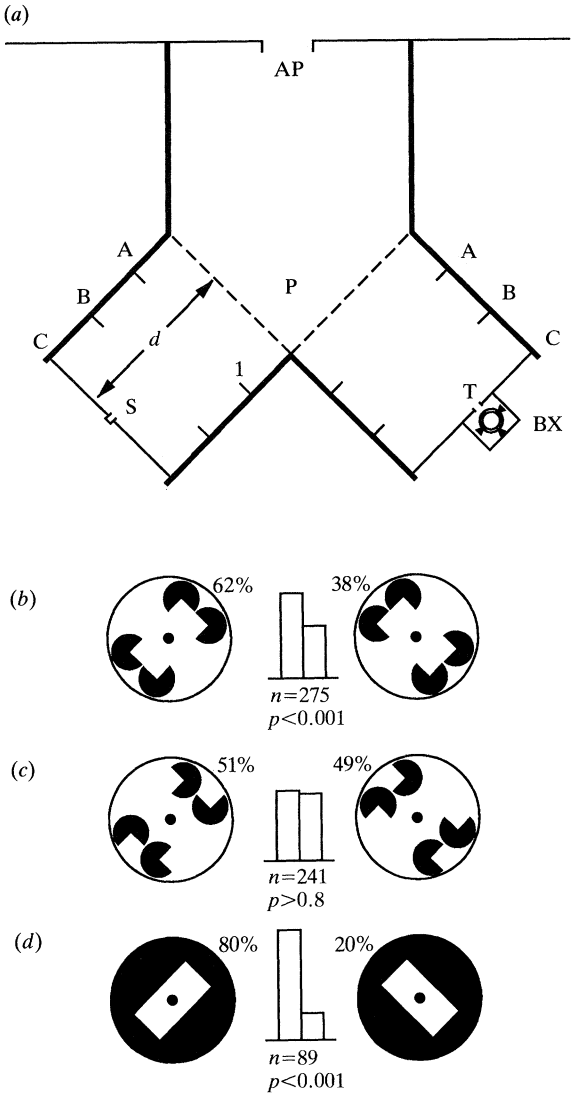

Figure 1. (*a*) The Y-shaped tunnel for training and testing. Bees enter through the window at AP from outside the laboratory and make their choice in the chamber at about P. The expected reward of sugar solution is found by entering the tube through the middle of the positive target into the reward box BX. (*b*) Bees trained to discriminate between regular striped patterns upwards to the right (positive) and downwards to the right (negative) are able to discriminate the (Kanizsa) illusory rectangles in (*b*) or the solid rectangles in (*d*) but they are not able to discriminate a similar pattern (*c*) when the illusion is spoiled by rotating some of the elements (*b–d* after van Hateren *et al.* 1990).

produced a contrast of at least 0.9. The discs were mounted 270 mm from the choice point P. The stripes in figure 2*a* had a period of 40 mm, subtending an angle of approximately 8.5° at the bees eye from the choice point; the bars in figures 2*b–d*, 3*a* and 4*a* had a width of 15 mm and could be resolved well by the bees. Previous experiments have shown that bees can distinguish the angle in a regular striped pattern of period down to 4° at the eye (Srinivasan & Lehrer 1988).

The training and test procedure was exactly as described in previous experiments (Srinivasan & Lehrer 1988; van Hateren *et al.* 1990; Horridge *et al.* 1992; Zhang *et al.* 1992). The main points are that (i) the training patterns are interchanged between the two sides when the small group of working bees have made two or three visits, (ii) controls and statistical tests can be devised to meet appropriate criticisms. The bees were at first trained on the vertical and horizontal striped pattern (figure 2*a*) until they reached over 80% success on periodic tests with or without a reward and then they were tested with the pairs of patterns with illusory contours, as shown in figure 2. In the second series of experiments (figures 3, 4), the bees were trained on the direction of the illusory contour and then tested for preference for horizontal or vertical. The criterion for a successful choice was whether the bee crossed the entrance of the tunnel. Bees which enter the wrong tunnel, discover their error and retrace their steps, scored negative, which makes the test more difficult but more reliable. The test patterns are switched between sides so that no bee is tested more than twice consecutively on the same side.

(*a*) *Electrophysiology*

Neurons of the lobula of the dragonfly *Hemicordulia tau* were probed with intracellular microelectrodes filled with 0.1 M lithium chloride. Techniques were standard for all recording and data processing. Peri-stimulus time histograms were plotted for a directionally selective unit which was tested with the appropriate stimulus combinations (figure 5). The stimulus for the electrophysiology was drawn with black ink on a translucent screen which was moved by a high-speed stepper motor behind a window, under computer control. The screen was illuminated from behind by a 75 W xenon arc lamp, and had a luminosity of 30 lux. The neuron type was discovered as part of a survey of neurons of the dragonfly lobula (O'Carroll 1992).

3. RESULTS

(*a*) *Testing bees with illusory contours*

The bees were trained with the horizontal stripes positive and the vertical stripes negative (figure 2*a*) and then tested on pairs of patterns which contain illusory contours that are clearly horizontal or vertical for the human visual system (figure 2*b–f*). In the patterns in figure 2*b–d* the striped pattern is at 45° or 135° and is identical on the two sides so that it offers neither horizontal nor vertical clue. The difference between figure 2*b* and figure 2*d* is that the bars have square ends in the latter and chisel-shaped ends in the former. This was an effort to get away from the formation of new aligned edges and from areas of different average brightness. The modification appears to make no difference to the performance. The difference between figure 2*c* and figure 2*d* is that the negative patterns are mirror images of each other, again as a control against giving horizontal or vertical clues.

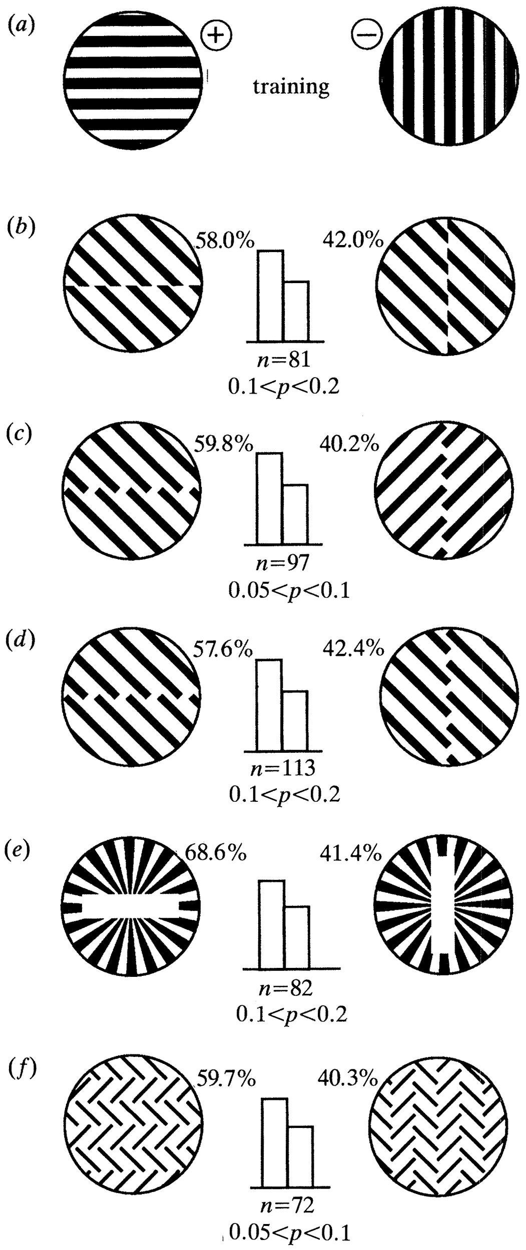

Figure 2. Patterns used for training and testing for discrimination of illusory contours. Results are given as percentages. (*a*) Bees were trained on horizontal (positive) and vertical (negative) stripes of period 8.5° subtended at the eye from the choice point. (*b–d*) Test patterns with illusory fault-lines in striped patterns. The stripes are at an angle which gives no clue about horizontal or vertical. (*e*) An illusory rectangle. (*f*) A texture that produces illusory boundaries which are either horizontal or vertical. In these experiments the training task is easy but the tests of discrimination are difficult and performance is low.

The textures in figure 2*f* are clearly more difficult for the bee, and presumably the bees use as a cue the low spatial frequencies that become apparent to us when we blur our eyes. These components arise because the ends of the bars are closer together than their middles, but it is hard to control against such effects without introducing new components in two-dimensional patterns. In the experiments in figure 2, the training task is easy but the test discriminations are difficult and cluttered by much irrelevant detail.

(*b*) *Training bees with illusory contours*

Instead of the protocol summarized in figure 2, we next trained the bees with the pattern containing the illusory contour and tested with a choice between a horizontal and vertical pattern (figures 3 and 4). The regular striped pattern used in training must be oblique to give no clue about horizontal or vertical, and the same on both targets, so offering no clue. The bees were therefore trained on the task of seeing the illusory contour. The subsequent tests on the horizontal and vertical bar (figures 3*b* and 4*b*) are easy whereas the tests in figure 2 are more difficult.

In the first series (figure 3), we trained with the positive illusory contour horizontal; in the second series (figure 4) the positive illusory contour was vertical. The results, with choice frequencies of 64% and 65% respectively are consistently better than those with the illusory contour as the test target.

The same bees, trained in the same way, were then tested with horizontal and vertical regular striped patterns (figures 3*c* and 4*c*), but they did not perform as well as with single bars. This is readily explained by the fact that the bar is a closer approximation to the illusory contour than is the striped pattern, assuming

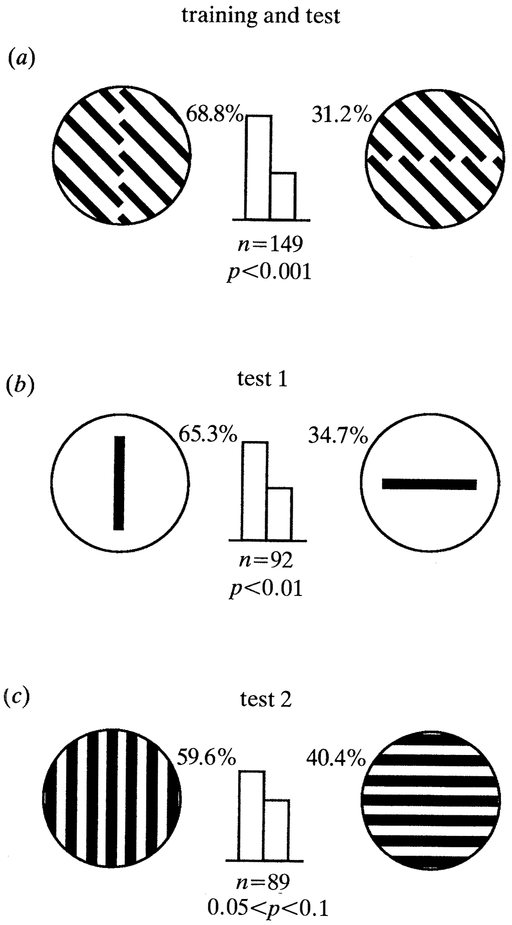

Figure 3. Bees were trained to discriminate between two oblique striped patterns, one (positive) containing a vertical and the other (negative) a horizontal illusory contour. They were then given tests to see whether they prefer horizontal or vertical with (*b*) single bar and (*c*) regular stripes of period 8.5°. In this experiment the training task is difficult but the discrimination test is easy.

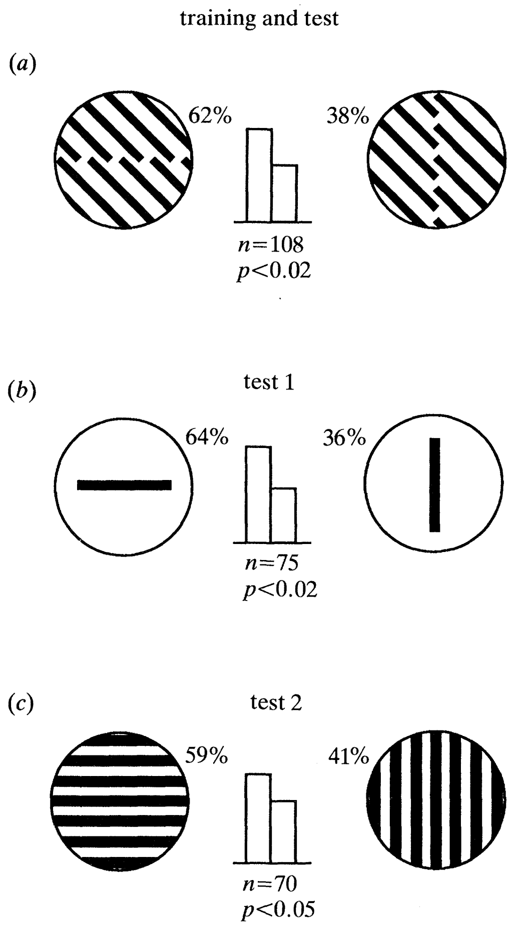

Figure 4. As in figure 3, but the positive target now had a horizontal fault line and the negative target a vertical one. Performance, as in figure 3, is better than when the protocol is reversed as in figure 2.

that the bees select the better approximation to the target on which they have been trained. A test with regular vertical and horizontal stripes must be confusing to a bee trained on targets that consist mainly of regular oblique stripes at 45°.

(*c*) *An appropriate neuron in the dragonfly lobula*

In the course of a survey of neurons of the lobula of the common local dragonfly *Hemicordulia tau*, a type was discovered which is sensitive to motion of a line but inhibited by whole-field motion of parallel stripes. Most of the cells encountered are non-directional, in that the direction of motion or the inclination of the line to the horizontal are not obviously important for the stimulation of the neurons. Some of these neurons respond to imaginary contours. One type, of particular interest, because it is directional, is illustrated in figure 5. The figure shows peri-stimulus time histograms, with spikes collected into 50 ms bins, from a directionally-selective, bar-sensitive unit.

The neuron responds strongly to the motion of a vertical black line to the left but weakly to its motion to the right. The response increases in strength as the line is progressively thickened and is strongest of all with a single edge of advancing darkening. It is inhibited slightly by motion of a whole field of parallel vertical stripes moving either way. When tested with a fault line in a striped pattern it responds directionally to the motion of the illusory contour as if to a line, but the response is abolished if the bars are interlaced (figure 5*d*), which also destroys the illusion of a vertical contour.

4. DISCUSSION

One might make the remark that the bees do not perform very well when tested on the illusory contours, even though repeated tests produce significant results. The reason seems to be that there is very little in the test patterns that corresponds to the horizontal and vertical stripes on which the bees have been trained. The bees perform better when trained on the illusory contour and tested on the horizontal versus vertical bar, which is an easier test.

To postulate a mechanistic explanation, we must make the assumption that there is some kind of repeated local template in the bees visual processing mechanism which is excited by the pattern which is remembered; call them templates or unit mnemons or what you wish. In the tests, the bees are forced to make a decision based on whatever cues they can find. It is known that bees can learn more than one cue and then make use of whichever cue is available (Zhang *et al.* 1992). The performance of bees in visual discrimination tasks certainly depends on how closely the targets presented in the test correspond to those in the training program, and performance also is reduced by testing with patterns that are divided into different regions where the spatial layout is relevant to the discrimination (Zhang & Horridge 1992). Our general idea of the learning mechanism is that each pattern excites a particular combination of elementary spatiotemporal templates, none of which carry much information on their own (Horridge 1991) and that learning a pattern is some of kind of retention of this combination, followed by a discrimination of the combination of templates excited by the test stimulus. Performance is then dependent on how many of the original combinations are excited, on average, by the test stimulus. It is to be expected, on this theory, that tests with illusory contours result in poorer performance than training with illusory contours. We have little idea what they see but the result leads directly into the question of neural mechanisms.

The explanation of the illusory contours seen by man in the patterns illustrated is that in the visual cortex of the monkey and presumably man, is a well-described group of neurons which detect stopped edges and lines, each along a particular orientation. A stopped edge or line is one which terminates. The ad-hoc explanation of illusory contours is that there are hard-wired higher-order neurons which are sensitive to the lining up of stopped ends, each along a particular orientation. Examples of these higher-order neurons have been recorded and partially characterized in monkey prestriate area V2 (von der Heydt & Peterhans 1989). In addition, there are local changes in psychophysical thresholds (Dresp & Bonnet 1991). An alternative theory, for which there is much varied

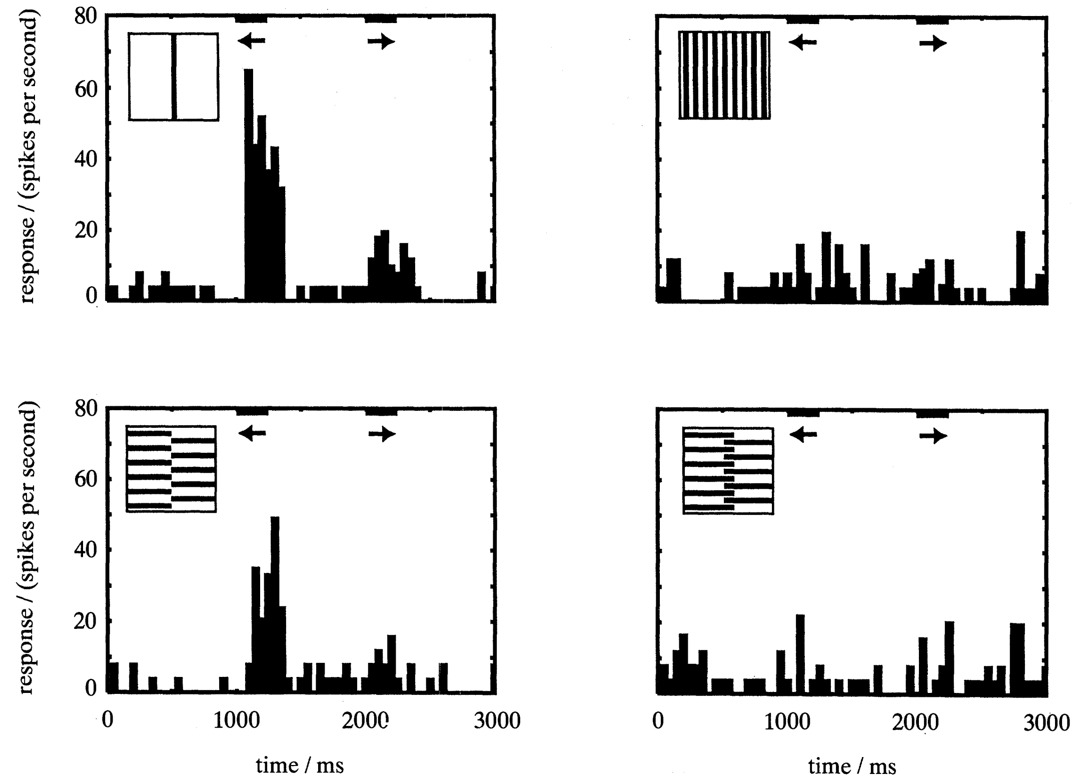

Figure 5. Post-stimulus histograms of spike responses of a lobula neuron of *Hemicordulia tau*. Each histogram is the average of five presentations at 10 s intervals. The stimulus was moved for 250 ms at 50° s^{-1}, first in the preferred, then in the anti-preferred direction. The neuron responds directionally to the single bar and the fault-line in the stripes, but not to the whole field of vertical stripes or to the fault-line when the stripe ends are overlapped.

evidence, is that these neurons are a by-product of the formation of temporary networks which assemble themselves when presented with a pattern. This so-called soft-wired system has not yet been identified in insects.

In insects there are plenty of neurons, at the lobula level and below, which respond to small objects moving anywhere in a large field. They tend to be phasic, easily habituated non-directional, insensitive to brightness, saturating at low contrast threshold and not purely green-sensitive like the directional motion perception system. Most are insensitive to whole-field motion of a patterned background, and some respond to the motion of a small target which moves over a moving patterned background (Rowell *et al.* 1977; Olberg 1981, 1986). In the fly there are similar neurons which respond to short bars but not long ones (Egelhaaf 1985).

The behaviour of these insect object-detector neurons strongly suggests that they have numerous inputs from small-field neurons of the medulla or lobula that detect any small moving contrast in their field, but that each large-field object-detector includes widespread inhibitory processes that feed back to all small-field neurons and inhibit them in a winner-takes-all situation. Such a circuit has been proposed as a mechanism for the inputs of the DCMD neuron of the locust (by, for example, Horridge (1978, figure 27), and discussed by Egelhaaf (1985)).

Whatever theory of object segmentation we accept, we might suppose that our experimental results suggest that the mechanisms of object segmentation and seeing boundaries is similar in bees and man, and can perhaps be extended to other insects and vertebrates. That conclusion is unfortunately also an illusion because insect and mammalian systems are adapted by long evolution to the natural properties of the visual world. Insects and primates appear to have neurons that are hard-wired for illusory contours but they might also have soft-wired systems that temporarily construct a model of the visual image in the visual processing mechanism. The principle of making use of illusory contours does not necessarily identify the neuronal subsystems. There does not have to be only one possible mechanism for seeing boundaries, and if there are totally different mechanisms in bees and man they are likely to yield the same visual illusions and there are also likely to be neurons in bee and monkey which behave in the same way as does the whole animal. Arguing from illusions to ad-hoc mechanisms is an uncertain investment where there are many processing pathways in parallel: all acted upon by Darwinian selection that evolves a satisfactory performance irrespective of the neuronal mechanism.

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