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Edge Detection by Landing Honeybees: Behavioural Analysis and Model Simulations of the Underlying Mechanism

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The mechanism of edge detection in the honeybee was investigated by examining the effects of combining different kinds of visual cues that define an edge. Free-flying bees were trained to land at three different types of edges which were defined by texture and relative motion cues either in isolation or in combination with each other. Bees are able to detect and land at the three types of edges, but do so with different frequencies. In contrast to the naïve expectation that edges jointly defined by two cues can be detected better than those defined by a single cue in isolation, the combination of the cues does not increase and may even decrease the detectability of an edge. When bees land at an edge the orientation of their body axis is strongly affected by the visual cues defining this edge. Model simulations were performed to test whether the experimental findings can be explained on the basis of a single edge detection mechanism sensitive to both types of visual cues. In the model, the information from both types of cues is sensed by two fields of movement detectors that receive their input signals from two adjacent patches in the visual field. The output of all detectors subserving either patch is pooled by integrating cells. The signals of the two integrating cells subserving the two adjacent patches are compared at a subtraction stage. The resulting signal is then rectified and forms the output signal of the model. The model simulations closely resemble the experimental results, thus providing evidence that edge detection by the bee could be mediated by a single mechanism. © 1997 Elsevier Science Ltd.

Vision Behaviour Model Edge detection Insect

INTRODUCTION

The boundaries of objects are of major importance in a variety of visual tasks ranging from image segmentation to figure–ground discrimination (eg. Bravo & Blake, 1992; Peterson & Gibson, 1994; Grossberg, 1996). The list of potential cues enabling the detection of a boundary includes such obvious ones as differences in colour, brightness or texture between object and background. There are, however, less obvious cues that can also be used by an animal to segregate figure from background. For example, the velocities of the retinal images of a nearby object and its distant background differ when an animal moves around in its environment (Gibson, 1950), giving rise to motion discontinuities at the boundaries of the object. These motion discontinuities have been demonstrated to be a reliable and sufficient cue for figure–ground segregation in insects (e.g. Reichardt & Poggio, 1979; Srinivasan *et al.*, 1990; Kimmerle *et al.*, 1996) and man (e.g. Regan & Beverley, 1984). Moreover, in electrophysiological experiments neurons have been found in the visual systems of a wide range of animal species that respond best to motion of a small object relative to its background (eg. Allman *et al.*, 1985; Egelhaaf, 1985; Frost, 1986). These neurons are believed to be elements of neuronal circuits concerned with figure–ground segregation.

In most studies investigating the mechanisms underlying edge detection, one of the above mentioned cues is presented in isolation at a given time. Under natural conditions, however, edges are usually defined by more than one cue. The present study analyses possible interactions of various visual cues in the detection of object boundaries by behavioural experiments with freely flying honeybees. Bees are well suited for such an analysis. It has been shown in earlier studies that they can detect edges defined by either texture or relative motion cues (Lehrer *et al.*, 1990; Srinivasan *et al.*, 1990; Lehrer & Srinivasan, 1993). These cues can be combined easily by the experimenter to obtain an edge that is defined

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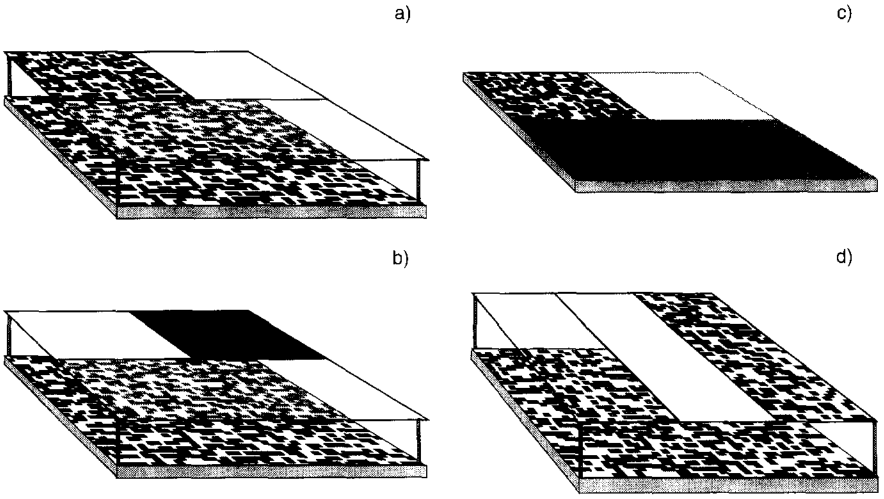

FIGURE 1. Schematic drawing of the experimental set-ups (not to scale). (a)–(c) Set-ups used to determine the detectability of various types of edges presented simultaneously. In (a) and (b), two square papers were attached adjacent to each other on the underside of a sheet of perspex raised above a randomly textured platform, half of which could be seen through the part of the perspex that remained transparent. In some of the experiments with the set-up shown in (a), a black square was used instead of the white one. (c) Four square papers were attached adjacent to each other on the underside of a sheet of perspex placed directly on the platform. No part of the perspex remained transparent. (d) Set-up used for training bees selectively to one of two simultaneously presented edges. Two strips of paper were attached adjacent to each other on the underside of a sheet of perspex raised above a randomly textured platform. One-third of the perspex remained transparent.

simultaneously by texture and relative motion. Moreover, bees can even be trained to find the boundaries of objects and to land at them (Lehrer & Srinivasan, 1993). Since the trained bees are foraging when performing the task, they are highly motivated and return to the experimental site repeatedly. Hence, a number of tests can be conducted with the same bee.

In the first part of our analysis we investigate whether bees prefer edges defined by cues presented in isolation or in combination with each other, in order to discover possible interactions between them. In the second part, a simple model is proposed to explain the major experimental data. The model is based on the assumption that texture and relative motion cues are processed by a single edge detection mechanism, sensitive to both cues simultaneously, rather than by two separate edge detection mechanisms, each sensitive to exclusively one of the two cues. This assumption is tested and confirmed by final behavioural experiments in which bees were selectively trained to land on edges defined by a particular type of cue.

MATERIALS AND METHODS

Experiments were performed on individually marked bees. In summer, their outdoor hive was located 30 m from the experimental site, in winter the distance between indoor hive and experimental site was 4 m. Note that the results of the experiments performed in the two seasons indicate that the behaviour of the bees was not affected by the difference in foraging distance. The experimental apparatus was surrounded by a large mosquito net in order to prevent newly recruited bees from entering the apparatus and interfering with the experiments. Trained bees entered the net through a small hole (about 10 cm in diameter) cut in the mesh. This entrance could be opened and closed by the experimenter, for example, to allow only one trained bee at a time to enter the apparatus during tests. The apparatus was placed on a flat turntable that could be rotated about its centre in order to change the orientation of the apparatus with respect to external landmarks and the net entrance.

Set-ups

The basic apparatus was a modified version of the set-up already used in former experiments on edge detection in bees (Lehrer & Srinivasan, 1993; their Fig. 7). Basically, it consisted of a sheet of perspex (50 cm × 50 cm) positioned above a wooden platform of the same size (Fig. 1). The height difference between perspex and platform could be varied. In the majority of experiments the wooden platform carried a black-and-white random texture (pixel size 3 mm × 3 mm). To eliminate external visual cues, the apparatus was surrounded by cardboard walls extending 3 cm above the perspex (not shown in figures). In different experiments, various modifications of this set-up were employed.

Set-up A. A homogeneously black or white and a randomly textured (pixel size 3 mm × 3 mm) square paper (each 25 cm × 25 cm) were attached adjacent to each other on the underside of the raised perspex sheet [Fig. 1(a)]. The bees could view the pattern on the lower platform through the half of the perspex that remained transparent. Three types of boundaries resulted from this arrangement: a boundary defined by the texture difference between the homogeneous and the textured surface (*texture edge*), a boundary defined by relative motion between the lower and the upper texture (*relative motion* *edge*), and a boundary defined by the combination of both of these cues (*combined edge*). Note that (i) the textured and the homogeneous surface are not identically bright; and (ii) the apparent size of the elements within the lower and raised texture is different. However, neither of these potential cues seems to be very important to edge detection (see Discussion).

Set-up B. A homogeneously white and black square were attached adjacent to each other on the underside of the raised perspex [Fig. 1(b)]. This modification resulted in the following three types of boundaries: one boundary defined by the brightness difference between the homogeneously white and black squares (*brightness edge*), and two other boundaries each of which was defined by two cues in combination (*combined edge*), i.e. the texture difference and the relative motion between the lower textured surface and the raised homogeneously black or white square, respectively.

Set-up C. Four squares (each 25 cm × 25 cm) were attached to the underside of the perspex [Fig. 1(c)]. In this case the perspex was placed directly on the platform. Edges were defined by brightness or texture differences only. Four types of edges were created: white/texture, white/grey, black/texture, and black/grey. The brightness edges (white/grey, black/grey) were characterized by nearly the same absolute brightness gradient as the texture edges (white/texture, black/texture) but lacked the texture difference. The relative luminances of the white, black, grey and textured squares were 1, 0.05, 0.44 and 0.48, respectively.

Set-up D. The perspex was subdivided into three parallel regions of equal size [Fig. 1(d)]. A white and a textured strip of paper (each 16.7 cm × 50 cm) were attached adjacent to each other on the underside of the perspex sheet. Through the third of the perspex that remained transparent, the bees could view the pattern on the platform 3 cm below. The two strips were attached in two different ways: either the textured strip covered an outer third of the perspex area and the white one the middle third [Fig. 1(d)], or vice versa [not shown in Fig. 1(d)]. In both cases, two edges were formed. In the second, the "priming version" (see below), the raised white and textured strip formed a texture edge, whereas the raised and the lower texture formed a relative motion edge. The priming was carried out to make the bees learn that there were two different edges to choose from. The presence of two different edges was very distinct in the priming version, as one was a texture edge whilst the other one was a relative motion edge. In the first version of set-up D, which was the ultimate training and test version, the raised textured and white strip formed a texture edge, whereas the raised white and the lower textured surface formed a combined edge, defined by both texture and relative motion cues [Fig. 1(d)]. In addition to the perspex sheet carrying the paper strips a second sheet of perspex, the complete area of which was transparent, was placed 1 cm above the first one [not shown in Fig. 1(d)]. The latter could be rotated with respect to the former one in steps of 90 deg in the horizontal plane. The reason for this measure will be given below.

Training and test procedures

In general, bees were trained solely or in groups of between three and five individuals. At every visit, they collected a reward from a small drop of sugar water which was placed on a sheet of perspex ("training perspex") at a randomly chosen spot along one of the boundaries. In order to ensure that bees were trained to find the boundaries, and not simply a drop, small drops of plain water were offered as well at other locations on the perspex sheet (see below). When all bees had received at least one reward, the perspex was cleaned with a wet sponge cloth and, from time to time, with absolute ethanol. Fluid was removed with cellulose tissue. In addition, the orientation of the whole apparatus with respect to its surround was frequently changed (see below).

Tests were started after several training visits and subsequently interspersed between training visits at regular intervals. Intervals were at least 2 hr or until each bee had been rewarded about 20 times. Tests lasted from 2 to 10 min depending on the total number of bees taking part in a given experiment. Bees were tested individually. However, a given bee did not necessarily take part in all of the tests. No reward was offered during tests. The orientation of the apparatus during a test did not coincide with the orientation during the immediately preceding training visit. The perspex on top of the apparatus used in the tests ("test perspex") was a different one than that used during training, but carried the identical papers (top perspex of set-up D was completely transparent; see above). Despite the fact that the two sheets of perspex used during training and test, respectively, were optically identical, bees tended to refuse to land on the test perspex at all. This could be overcome to a certain degree by "cleaning" the test perspex immediately before each test with the same sponge as the training perspex. We assume that this measure made the test perspex more acceptable with respect to seemingly important general olfactory properties. It should be noted that this measure simply increased the overall attractiveness of the test apparatus and did not provide any cue that facilitated the detection of edges. In general, a new group of bees was trained in each experiment. Some experiments were repeated with a second group of bees. This control ensured that the results obtained did not depend on the group of bees taking part in a given experiment.

In addition to these general procedures applying to all experiments, specific procedures were used in single experiments and set-ups, respectively. These will be described separately below.

With set-ups A and B the small drops of plain water, offered to ensure that bees were trained to find the boundaries, and not simply a drop, were placed at random locations on the perspex but well away from the boundaries. Between consecutive training visits the azimuthal orientation of the whole apparatus was changed in eight equidistant steps. In addition, the reward was moved from one edge type to the other. The succession of the 24 possible combinations of orientation and type of rewarded boundary (3 edge types × 8 orientations) was pseudo-random. That is, all 24 combinations were present in a series of 24 consecutive training visits. After each bee had received at least 24 rewards, tests were interspersed at regular intervals between the training visits. The tests were also performed at eight different, equidistant orientations of the apparatus.

In experiments performed with set-up C, the training and test procedures employed with set-ups A and B were modified to accommodate the increased number of edges. In particular, tests started only after each bee had received at least 32 (8 × 4) rewards.

The training and test procedures employed with set-up D were rather different. Since the question in this experiment was whether bees can discriminate between two types of edges presented simultaneously, they were rewarded only at one type of edge. A small drop of plain water was offered at the unrewarded edge. At the beginning of the training the priming version of set-up D was employed. On average, bees were rewarded 64 times exclusively at the relative motion edge, formed by the raised and the lower texture, in order to "prime" the bees to the relative motion cue. This was done since it has been shown that priming can enhance the performance of bees in discrimination tasks (Zhang & Srinivasan, 1994). Here, we did not evaluate the consequences of priming on the performance of the bees. After the priming phase the second version of set-up D was replaced by the first one [Fig. 1(d)]. Bees were rewarded at least 24 times at the combined edge, formed by the raised white and the lower textured surfaces, before tests were interspersed. In total, bees received more than 150 rewards at the combined edge during this phase of the experiment. After a sufficient number of tests had been performed bees were trained to find the reward at the texture edge, formed by the raised textured and the white strip. Again, bees were rewarded at least 24 times before tests were interspersed. Eventually, each bee in this phase of the experiment also received more than 150 rewards. Bees performing this experiment were trained and tested at four or eight equidistant orientations of the apparatus with respect to its surround. The succession of orientations again was pseudo-random. In addition to changing the orientation of the whole apparatus the uppermost perspex sheet (see above), carrying the reward, was rotated with respect to the lower perspex sheet, carrying the stimulus, in a pseudo-random manner in steps of 90 deg. This measure was taken to make potential olfactory cues worthless during training. A fresh "test perspex" sheet was used during tests.

Data evaluation

Landings at boundaries were recorded by the experimenter on a microtape specifying the type of boundary and the orientation of the body axis of the bee with respect to the boundary. Orientations of the body axis at each edge were classified into two groups only. For example, at the relative motion edge, bees were recorded as directed towards the raised or towards the lower textured area. In general, this distinction could be made quite easily. When interpreting the results it was assumed that the number of landings at each edge is proportional to its detectability.

The frequency of landings at each boundary ("choice frequency") was calculated separately for each bee as the percentage of the total number of landings of the bee. Subsequently, the average choice frequency for each edge was calculated from the values obtained from different bees. Also, the frequency of landings with the bee oriented in either of the two classified directions was calculated separately for each bee. The frequency of landings at each edge in the two directions add up to 100%. The average frequency of landing directions at each edge was calculated from the values obtained from different bees. Standard errors were corrected for small sample sizes (Sokal & Rohlf, 1981). In one case, the numbers of landings at two edges were tested for a significant difference by means of the Mann–Whitney *U*-Test (Rohlf & Sokal, 1981; Sokal & Rohlf, 1981).

Model simulations

Model simulations were performed on 386 and 486 PCs. The simulation program was written in Borland-Pascal (Borland). Details of the program are specified in the Results section.

RESULTS

Behavioural experiments: spontaneous edge preferences

We began our examination by determining the landing frequencies at three different types of boundaries [set-up A, Fig. 1(a)]: (i) a boundary defined by a texture gradient (texture edge); (ii) a boundary defined by relative motion (relative motion edge); and (iii) a boundary defined by both cues simultaneously (combined edge). This experiment essentially involved comparing the spontaneous preferences for the three types of edges, since all edges were rewarded equally often during training. In the first series of experiments the height difference between raised perspex sheet and low platform was 5 cm. The texture edge was formed by a randomly textured square paper adjacent to either a homogeneously black or a homogeneously white square paper.

Bees landed at all three types of edges, though with different frequencies. With the homogeneously black square 45.4% of the landings were recorded at the texture edge, 36.4% at the relative motion edge, and only 18.2% at the combined edge [Fig. 2(a)]. Thus, under the assumption that landing propensity equals the detectability of an edge, the detectability of the combined edge, defined jointly by two cues, is poorer than the detectability of the edges offering a single cue in isolation. This finding is in contrast to the naïve expectation that the

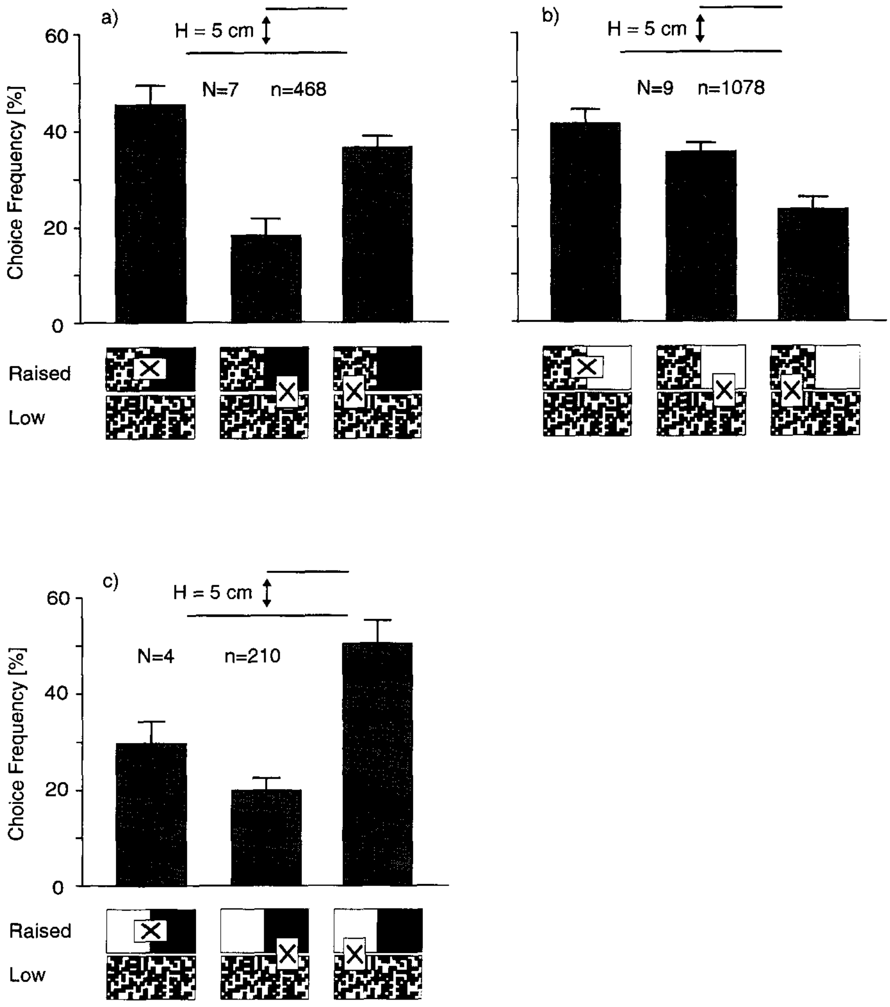

FIGURE 2. Choice frequencies (+SEM) for three different types of edges when the raised perspex sheet is 5 cm above the platform [see Fig. 1(a, b)]. Each bar denotes the choice frequency for the edge indicated by the cross in the insets along the abscissa. H = Height difference between raised perspex sheet and lower platform as indicated by the inset. N = number of bees taking part in the experiment, n = total number of landings that contributed to the displayed results. Note that the statistics have been performed on "N" rather than 'n'. Bees do not land equally often at all edges. (a, b) The detectability of the texture edge [left in (a) and (b)] is larger than the detectability of the combined edge [centre in (a) and (b)] though the latter is defined by an additional cue, indicating an opposing interference of the edge defining cues. Compared with the relative motion edge [right in (a) and (b)] the combined edge is less detectable only if it is defined by the black square, indicating differences between the processing of black and white, respectively. (c) The combined edge flanked by the white and the randomly textured surface is detected best (right), whereas the least landings were recorded at the combined edge flanked by the black square and the randomly textured surface (centre). The detectability of the edge formed by the raised white and black square (left) is intermediate.

detectability of an edge should increase by combining two cues which on their own are already sufficient for edge detection.

When the black square was replaced by a white one, the edge jointly defined by texture and motion still continued to attract fewer landings than the edge offering the texture cue alone [Fig. 2(b)]. However, in this case, the number of landings at the combined edge was larger than at the relative motion edge (35.3% vs 23.4%) but still somewhat smaller than at the texture edge (41.3%). Hence, bees seem to detect the combined edge more easily if it is associated with a white surface rather than a black one. In order to ensure that this difference is not simply due to unknown differences between the two groups of bees taking part in either experiment, a control experiment was performed [Fig. 2(c)]. A white and a black square were attached adjacent to each other on the underside of the sheet of perspex, which was raised 5 cm above the randomly textured platform [set-up B, Fig. 1(b)]. Again, bees landed much more often at the combined edge flanked by a textured and a white (50.4%) rather than by a textured and a black (19.9%) surface. Even the white/black edge was chosen more frequently (29.7%) than the combined edge formed with a black square. Furthermore, the choice frequency for a texture edge was much larger when the textured square was adjacent to a white (42.2%) rather than a black (23%) square (data not shown). Thus, white is indeed more effective than black in attracting landings when it is juxtaposed against a black-and-white texture to create an edge.

In order to characterize the landing behaviour of the bee at each edge, not only the relative frequencies of landings were taken into account. Rather the distributions of landing directions at each edge, that is the orientation of the longitudinal axis of the bee with respect to the boundary after landing, were also compared. In the experiment with set-up A and the homogeneously black square [Fig. 3(a)], bees were directed towards the textured side in 90.2% of the landings at the texture edge, and towards the raised side in 95.4% of the landings at the relative motion edge. The distribution of landing directions at the combined edge was intermediate, i.e., in 45.6% of the landings bees were directed towards the lower textured and in 54.4% of the landings towards the raised black surface [Fig. 3(a)].

A very similar distribution of landing directions was obtained when the black square was replaced by a white one [Fig. 3(b)]. Again, in almost all cases bees were oriented towards the textured (95.3%) and raised (94.4%) side at the texture and relative motion edge, respectively, whereas an intermediate distribution was recorded at the combined edge: in 37.6% of the landings bees were directed towards the lower textured and in 62.4% of the landings towards the raised white surface.

Interestingly, the extreme imbalance of landing directions in favour of the textured side at the texture edge holds regardless of the actual brightness gradient, i.e., with a white or a black square adjacent to the textured one. This finding suggests that texture is an important determinant of the landing behaviour of the bee at edges. The suggestion is substantiated by the results of a control experiment. Here, we not only recorded the landing directions of the bees at two different texture edges (black/texture, white/texture) but also at two different pure brightness edges (black/grey, white/grey), i.e., at edges defined by the same brightness gradient but lacking the texture difference [set-up C, Fig. 1(c)]. Again, distributions of landing directions at both of the texture edges were strongly imbalanced in favour of facing the textured square [Fig. 3(c)]. In contrast, at the pure brightness edges landing directions were distributed more symmetrically with a slight tendency to the extremes, i.e., bees tended to be oriented towards white at the white/grey edge and towards black at the black/grey edge.

The results presented so far suggest that at the combined edge the distribution of landing directions is affected by two conflicting tendencies: the first appears to induce the bees to land in the direction of the raised (homogeneously black or white) side of an edge. The second appears to lead to landing directions towards the textured (lower) side. The first tendency is due to the relative motion cue, the second one due to the texture cue. The intermediate distribution of landing directions at the combined edge then can be interpreted as the result of the interference between the two cues.

This interpretation is corroborated by the finding that the distributions of landing directions at the texture and combined edge become more similar when the height difference between perspex and platform (set-up A) is decreased to values of 2 and 1 cm and, therefore, the strength of the relative motion introduced by the bee when approaching and crossing the combined and relative motion edge is reduced (data not shown). In experiments with the black square, for instance, the relative numbers of bees directed towards the textured (lower) side of the combined edge were 45.6% at a height difference of 5 cm, 62.1% at 2 cm, and 74.3% at 1 cm. The corresponding frequencies of landings in the direction towards the textured side at the texture edge were 90.2%, 93.6% and 85.8%, respectively. A similar tendency holds for the landing distributions obtained in experiments with a white instead of a black square. In addition, the overall choice frequencies of the texture and combined edge become more similar and the choice frequency for the relative motion edge decreases (data not shown).

In conclusion, the combination of the texture and the relative motion cue has two obvious effects on the landing performance of bees when compared with the performance at edges that carry these cues in isolation: (i) it may dramatically decrease the overall number of landings; and (ii) it changes the distribution of landing directions.

Model simulations of an edge detection mechanism

We have demonstrated that, in edge detection by the bee, texture and motion cues might oppose each other, leading to an unexpectedly low detectability of the combined edge. In the next step of our analysis we asked how the two cues might interact. There are two principally different possibilities. (i) Texture and relative motion cues are processed in independent information channels and by separate edge detection mechanisms. Consequently, a texture and a relative motion edge are represented in two separate channels, and a combined edge is represented simultaneously in both channels. The type of cue defining an edge can be inferred from the presence or absence of activity in either channel. The information carried by the two channels interacts somewhere before the motor output. (ii) Only one edge detection mechanism exists. This mechanism is simultaneously sensitive to both texture as well as relative motion cues. Hence, all types of edges are represented by activity in the same channel, and the interaction of the cues is taking place at the level of the edge detection mechanism.

Model architecture and simulation procedure

Whereas, from an intuitive point of view, the first possibility is the more appealing one, since the cues are nicely separated from each other and thus easily accessible, it is the more implausible one in biological terms. This is because it has been demonstrated in several species that motion detection by biological motion detectors is rarely independent of, for instance, textural properties of the stimulus (for review, see Borst &

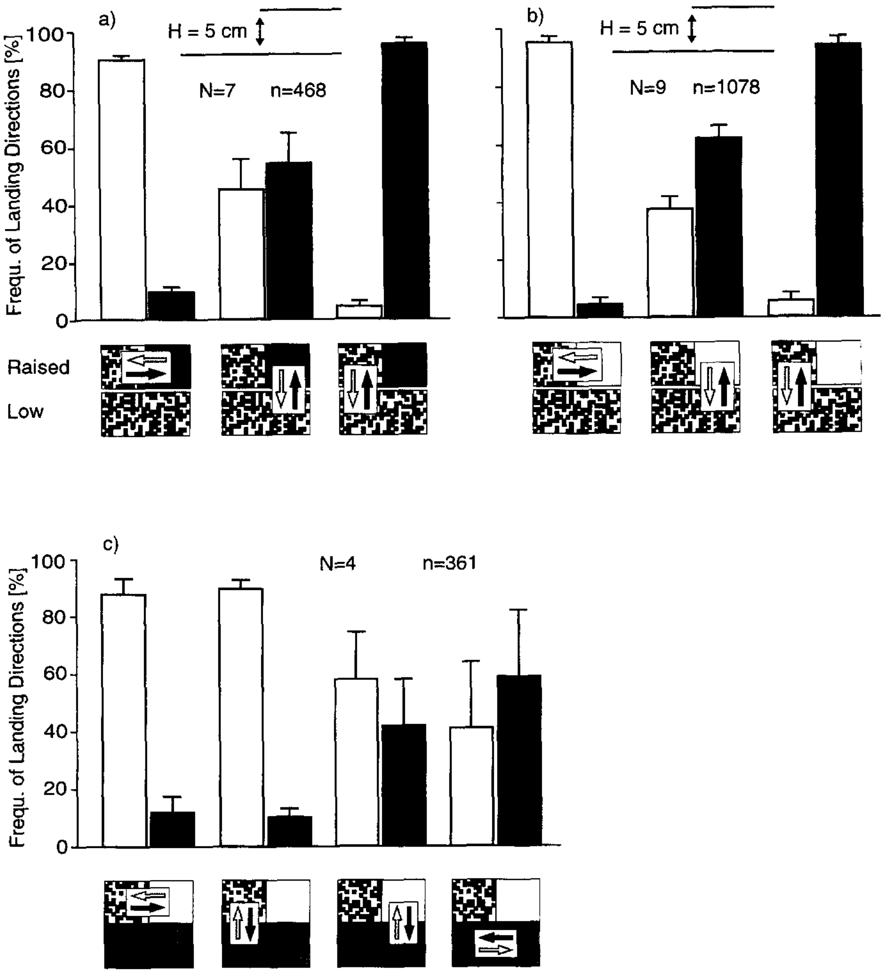

FIGURE 3. Frequencies of landing directions (+SEM) for three (a, b) or four (c) different types of edges with 5 cm (a, b) or without any (c) height difference between the perspex sheet and the platform [see Fig. 1(a, c), respectively]; bees oriented in one of two opposing directions. Each bar denotes the percentage of landings in a certain direction as indicated by the arrows in the insets along the abscissa. For other conventions see Fig. 2. (a, b) Data were obtained in the same experiments as those in Fig. 2(a, b). The distributions of landing directions are extremely one-sided at the texture edge [left in (a) and (b)] and at the relative motion edge [right in (a) and (b)], with the vast majority of landings directed towards the textured square and raised side, respectively. In contrast, at the combined edge [centre in (a) and (b)] the distribution of landing directions is more balanced. (c) Note that in this set of experiments the perspex was placed directly on the platform, i.e., there was no relative motion cue. At the two texture edges (left half) the distributions of landing directions are extremely one-sided in favour of the textured side. In contrast, bees were directed about equally often in both directions at the brightness edges (right half). Therefore, the textural properties and not the actual brightness gradient seem to be the major determinant of landing direction.

Egelhaaf, 1989). This also holds for the optomotor systems of insects (for review, see Egelhaaf & Borst, 1993) including the bee (Ibbotson, 1991). Therefore, our second hypothesis is worth exploring further through model simulations. Biological motion detectors, the outputs of which do not depend only on the velocity of the stimulus but also on its brightness, contrast, and spatial frequency, can be simulated by the so-called correlation-type movement detector (for review, see Egelhaaf & Borst, 1993). Therefore, we implemented the input elements of our model of the edge detection mechanism of the bee as correlation-type movement detectors.

The model is based on the notion that edges can be detected by comparing the motion signals from neighbouring elongated patches in the visual field, i.e., elongated areas flanking the edge (Fig. 4). Thirty topographically organized movement detectors subserve each of the two patches along the x-axis. Each movement detector consists of two mirror-symmetrical subunits. Each subunit has two input lines, measuring the light intensities at two neighbouring points in space (separation: 2.15 deg). In accordance with spatial sensitivity functions known in insect photoreceptors (Land, 1981; Warrant & McIntyre, 1993) the input signal is spatially low-pass filtered by a gaussian-like function (sigma 0.86 deg). In each detector subunit, the signals of the two input lines are multiplied with each other (M) after one of them has been delayed by a first-order low-pass filter. We have set the time constant (τ) of this filter to 40 msec. This value is well within the range of time constants experimentally determined in flies (de Ruyter van Steveninck *et al.*, 1986; Borst & Egelhaaf, 1987; Egelhaaf & Reichardt, 1987). Since the optimal temporal frequency of a moving stimulus is very similar for the steady state optomotor responses in the fly (Hausen, 1981) and the bee (Ibbotson, 1991), the size of the time constant in the movement detector input lines seems to be similar in both insect species. The output signals of the mirror-symmetrical subunits are further processed with opposite signs. The signal of the negative subunit (−) is weighted by a factor (0.8) before it is subtracted from the signal of the positive subunit (+) to form the final output signal of the detector. The imbalance between the subunits was necessary in order to ensure that the model produced a larger response to the texture edge than to the combined edge [see Fig. 2(a, b) and below]. Such an imbalance is not biologically implausible and is, in fact, suggested by the results of electrophysiological studies on the fly motion detecting system in combination with model simulations (Egelhaaf *et al.*, 1989). The signals of the detectors subserving each patch are integrated by "cells" with gaussian-like sensitivity characteristics (sigma: 12.9 deg). Finally, the output signals of the two integrating cells are subtracted from each other and the resulting signal is rectified to form the final output of the model. In the graphs this signal is shown after filtering with a 7-point triangular filter with weights 1/25, 3/25, 5/25, 7/25, 5/25, 3/25, 1/25 in order to smooth out high-frequency response fluctuations.

The results, presented in the section entitled "*Behavioural experiments: spontaneous edge preferences*", revealed that edges are treated qualitatively in the same way by the edge detection mechanism of the bee irrespective of the polarity of the respective brightness changes. In order to make the model edge detection mechanism perform similarly to the behaviour of the bee, we extended the model by introducing separate "On" and "Off" motion detectors subserving each location in the two patches (not shown in Fig. 4). The On and Off motion detectors have the same structure (as shown in Fig. 4) but differ only in the way their input signal is processed. In a first approximation, the input signals of the On motion detectors are not preprocessed at all and reflect the retinal brightness changes (after spatial filtering) as they are. In contrast, the input signals of the Off motion detectors are the input signals of the On motion detectors inverted around their mean value. The integrating cells sum up the output signals of the On and Off motion detectors. The signals of the latter are weighed by a factor of 0.9.

In the behavioural experiments the bees mostly flew very close to the perspex. For the simulations we assumed an altitude of 1 cm above the perspex. The height difference between the raised perspex and the lower platform was set to 3 cm, simulating a height difference between bee and raised pattern or platform of 1 or 4 cm, respectively. In accordance with the absolute size of single pixel elements in the real random texture (3 mm × 3 mm) the apparent size of these pixel elements is calculated as 16.7 deg for the simulated raised random texture and 4.3 deg for the pattern on the platform. The flight speed of the real bees varied. In the simulations we used two speeds, 10 and 30 cm/sec, representing slow- and fast-flying bees, respectively.

To simulate the retinal image displacements encountered by a bee when flying across the experimental apparatus, two sequences of pixels were moved in the visual field of the model bee. The sequences corresponded to one-dimensional sections of the retinal image that extend in the flight direction of the model bee. Motion was restricted to the x-axes of the receptive fields of the two integrating cells, i.e., along the axes of the motion detectors giving input to these cells. The intensity of the pixels following each other within either of the two sequences depended on the experimental situation that was simulated: they were all black, all white, or a series of black and white pixels of variable length following each other in random succession. In order to take the y-dimension of the fields of motion detectors into account, the calculation of the model output was repeated 200 times. Sequences corresponding to textured surfaces were generated anew each time. The model outputs of all runs were averaged subsequently. At the beginning of each simulation only one of the sequences was moved within the receptive fields of the integrating cells to obtain the model response to motion of one of the edge-forming surfaces only. In the course of the simulation a progressively larger part of the first sequence was substituted by a simultaneously extending part of the second one which was, thus, moving into the receptive fields of the integrating cells. Substitution started at the outer margin of the receptive field of one of the integrating cells and stopped when the transition between the two sequences reached the outer margin of the receptive field of the other cell. A sequence corresponding to a surface closer to the model bee moved faster through the receptive fields of the integrating cells than a sequence corresponding to a more distant surface. In effect, the procedure described above simulates the visual stimulus that would be experienced by a bee when it approaches and crosses an edge.

When simulating the approach to a texture edge and its subsequent crossing, both the homogeneous surface and the randomly textured one, i.e., the corresponding sequences of pixels, moved with the same (high) speed. In contrast, when simulating the crossing of an edge defined exclusively by relative motion, or jointly by relative motion and the texture cue, the surface supposed to be closer to the model bee, i.e., the raised surface, moved faster than the surface supposed to be more distant. Moreover, the raised surface "slipped" across the lower one due to its higher speed. Therefore, the boundary between the two surfaces was not fixed as in the case of a texture edge but changed in the course of the simulation. In other words, the simulation included the effects of occlusion or disocclusion of the lower texture by the raised surface.

Performance of the model

The model output at a given time depends on the types of surfaces currently "seen" by the two integrating cells

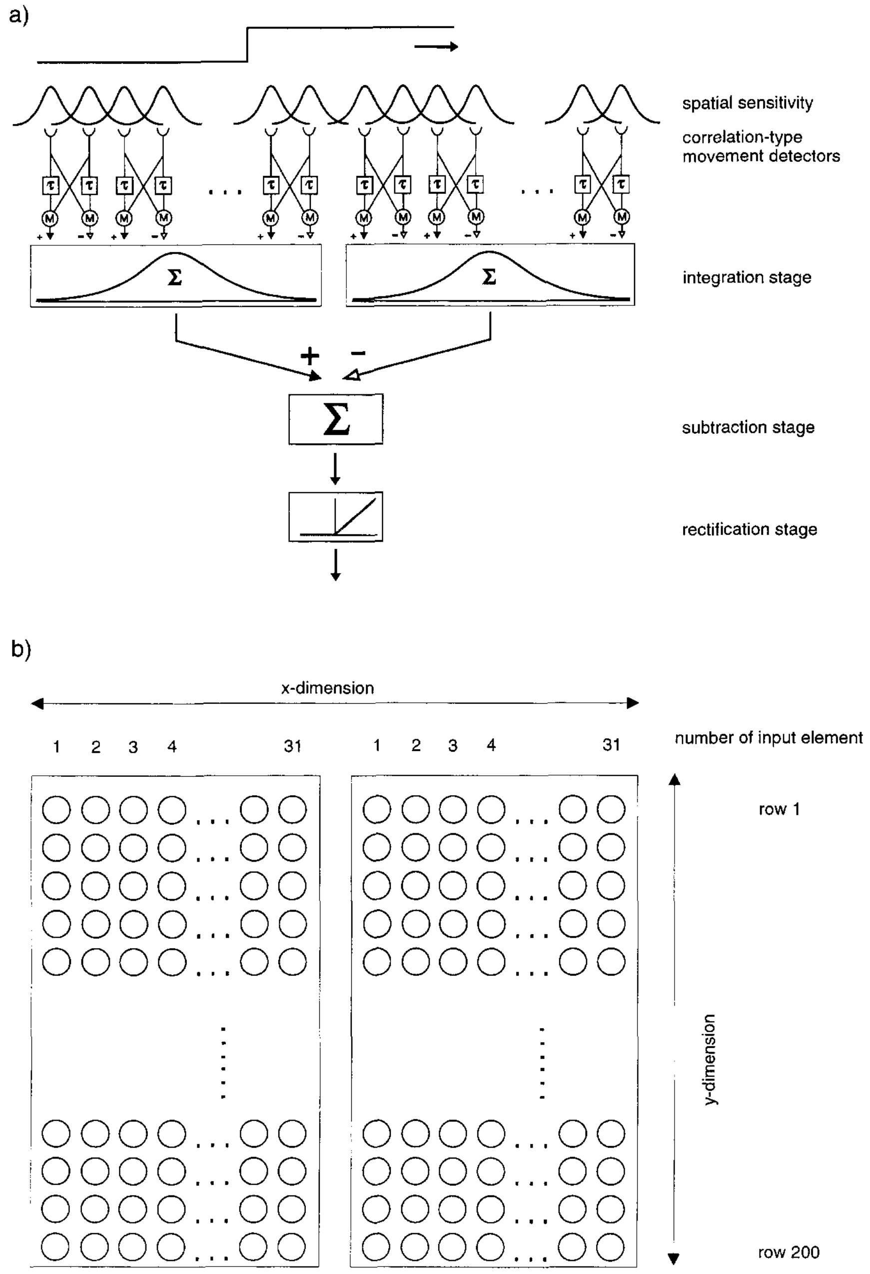

FIGURE 4. Scheme of the proposed edge detection mechanism. A moving edge is detected by comparing motion and textural information from two spatially displaced patches in the visual field. (a) Cross-section of the model along the *x*-axis. The proposed model can be divided into five processing stages. (τ) = first-order low-pass filter; (M) = multiplication; (Σ) = summation. The edge, i.e., a change in brightness, is indicated by the line on top of the figure, the direction of motion by the arrow. (b) Schematic drawing of the spatial arrangement of the input elements (circles) to the model mechanism, top view, with 31 input elements along the *x*-axis and 200 input elements along the *y*-axis. Motion of the pattern over the input elements was restricted to the *x*-dimension, i.e., perpendicular to the orientation of the moving edge. Further details in text.

(Figs 5–7). For instance, when the model bee approaches a texture edge from the homogeneous side, the model output is zero as long as only the homogeneous surface is within the receptive fields of both of the integrating cells [Fig. 5(a, b), first part of the response trace]. As soon as the textured surface enters the receptive field of one of the integrating cells, the model output suddenly increases. It reaches a peak value when the edge is in between the receptive fields of the two integrating cells and then decreases again [Fig. 5(a, b), central part of the response trace]. Finally, when the textured surface is seen by both integrating cells, the instantaneous model output fluctuates between zero and small positive values depending on the texture currently within the receptive field of either integrating cell [Fig. 5(a, b), final part of the response trace]. We took the strength of the response peak in the central part of the response trace as an indicator of whether the model bee had detected the edge. The larger the peak relative to the amplitude of the other response fluctuations, the more reliable the detection of the edge.

The model bee is able to detect all three simulated edge types, mimicking those used in the behavioural experi-

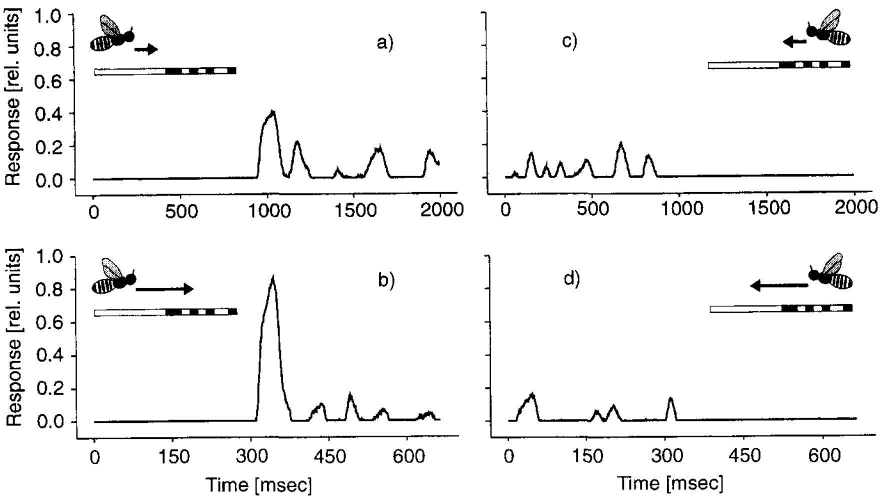

FIGURE 5. Simulations of the responses of the model edge detection mechanism when the model bee is flying across the texture edge. Flight direction and speed are indicated by orientation and length of arrows in insets, respectively. The model output is plotted vs time. It is normalized to the strongest response obtained in all of the simulations conducted. Note the different time scales in (a) and (c) versus (b) and (d) due to different speeds of the model bee. The model bee detects the edge only when approaching from the homogeneously white side (a, b). Performance is better when the model bee is flying rapidly (b).

ments. However, the detectability of each edge is different. Moreover, for a specific edge the model output, and thus the detectability of the edge, depends on the flight direction and speed of the model bee (Figs. 5–7).

The model bee detects the texture edge best when flying fast from the homogeneous surface towards the textured one [Fig. 5(b)]. The edge is less detectable when the model bee flies slowly, though still in the same direction [Fig. 5(a)]. When flying in the opposite direction, i.e., from the textured side towards the homogeneously coloured one, the texture edge is hardly detected, if at all. This holds regardless of the velocity of the model bee [Fig. 5(c, d)].

The detectability of the relative motion edge also depends on flight direction. The model output signals the edge only if the model bee is flying from the lower towards the raised pattern flanking the edge [Fig. 6(a, b)] and not when flying in the opposite direction [Fig. 6(c, d)]. In addition, this edge is detected better at the slower flight speed [compare Fig. 6(a and b)].

The detectability of the combined edge depends less on flight direction or flight velocity of the model bee than the detectability of the edges defined by a single cue only. Nevertheless, the model output differs for the four combinations of flight direction and speed (Fig. 7). It is strongest when the model bee crosses the edge from the lower towards the raised side and flies slowly [Fig. 7(a)]. Interestingly, a rapidly flying model bee detects the combined edge independently of the direction of approach [Fig. 7(b, d)]. When the model bee flies slowly and in the direction of the low pattern, the edge is not detected [Fig. 7(c)].

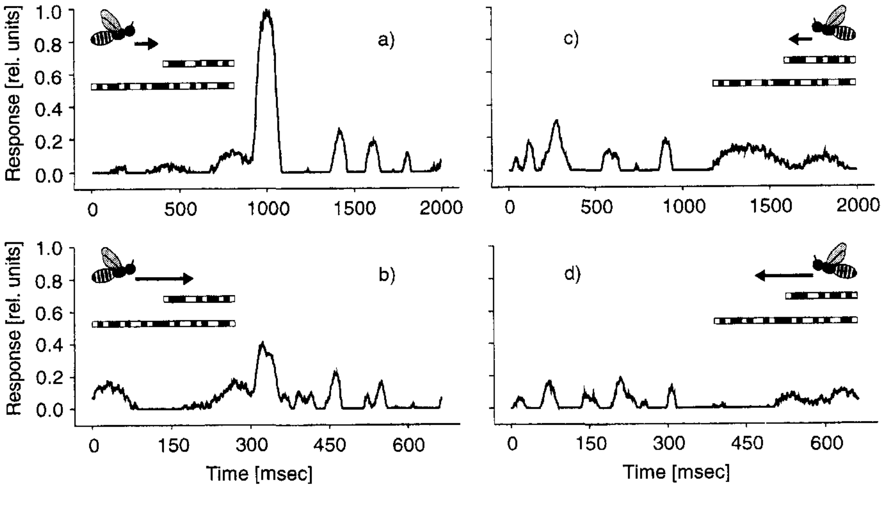

FIGURE 6. Simulations of the responses of the model edge detection mechanism when the model bee is flying across the relative motion edge. For conventions see Fig. 5. The model bee detects the edge only when approaching from the lower side (a, b). Performance is better when the model bee is flying slowly (a).

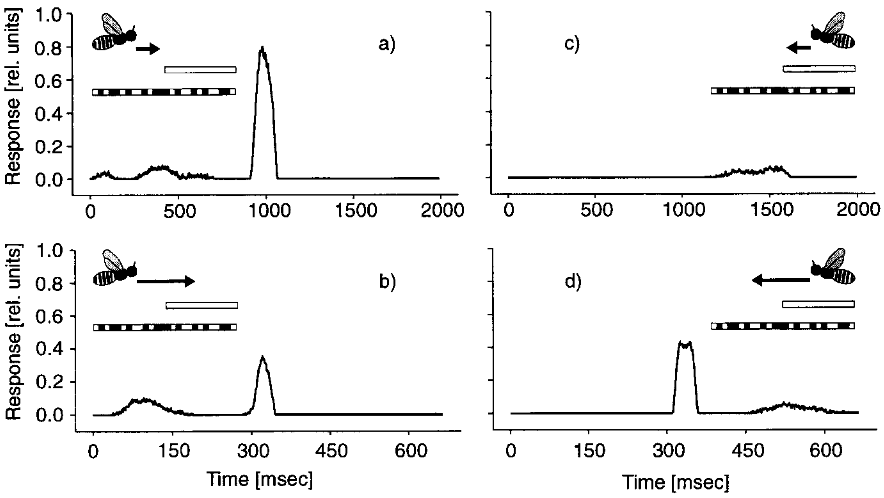

FIGURE 7. Simulations of the responses of the model edge detection mechanism when the model bee is flying across the combined edge. For conventions see Fig. 5. When flying slowly (a, c) the model bee detects the edge only when approaching from the lower textured side (a). Rapidly flying model bees (b, d) detect the combined edge regardless of direction of approach. Performance is best when the model bee is flying slowly and approaching from the lower textured side (a).

These features of the edge detection model display a remarkable resemblance to the main results of the behavioural experiments in which the height difference between perspex and platform was 5 cm and the relative motion cue was therefore strong. Thus, the majority of the behavioural results can be explained at least qualitatively on the basis of a single edge detection mechanism sensitive to both motion and texture cues.

Behavioural experiments: selective training to specific edges

In order to obtain experimental support in favour of the hypothesis that edge detection by the bee is mediated by a single mechanism we performed further experiments. In contrast to the experiments described earlier, where the bees were rewarded at all edge types offered simultaneously in order to compare spontaneous edge preferences, in the experiments described here bees were rewarded exclusively at one of two simultaneously presented edges, namely a texture and a combined edge, in order to examine whether they can learn to distinguish between the two edge types. If they learn to make the discrimination well, it is reasonable to conclude that bees are not using the same cue to detect the two edge types, and that at least two different types of cue are being sensed by different edge detection mechanisms. In contrast, if it is difficult to train bees to land preferentially at a particular edge type, it can be suggested that the edge defining visual cues are processed by a single edge detection mechanism.

Bees can be trained to discriminate between the combined and the texture edge. The choice frequencies for the combined edge under the two training conditions (i.e., with bees rewarded either at the combined or at the texture edge) are significantly different (Mann–Whitney U-test, $U_S = 23$, $P < 0.05$, $N = 5$): the mean choice frequency for the combined edge was 54.5% when the combined edge was rewarded and 37.2% when the texture edge was rewarded (Fig. 8).

However, the bees needed a large number of training visits, i.e., more than 150 rewards at either edge, to achieve the discrimination ability indicated by the choice frequencies. Therefore, the performance of the bees in the present task can be regarded as poor. This is particularly obvious if we compare the performance in the task described here to the performance of bees in, for example, colour learning. In colour discrimination tasks the choice frequency for the rewarded colour can exceed 90% even after as few as two or three rewards (Opfinger, 1931; Menzel, 1967). The performance of the bees in the present task is more comparable to that observed when bees are required to distinguish between different grey levels (Hörmann, 1935). Here, bees have to be trained up to a day before they choose the specific grey level to which they were trained distinctly more often than other grey levels. Most likely, grey levels are processed by a single information channel. Therefore, the only way to distinguish between grey levels is in terms of the strength of the signal produced by this channel. This is similar to the recognition of a certain type of edge if our hypothesis that different types of edges are detected by a single edge detection mechanism was correct. This task seems to be more difficult than the discrimination of colours that is based on more than one colour channel.

DISCUSSION

In behavioural experiments we investigated the effects of combining various visual cues on the ability of landing honeybees to detect edges. We focused on two edge defining cues—texture and relative motion—presented in isolation or in combination with each other. On the basis of the experimental results we propose a simple model of the edge detection mechanism of the bee which was tested by computer simulations. The close correspon-

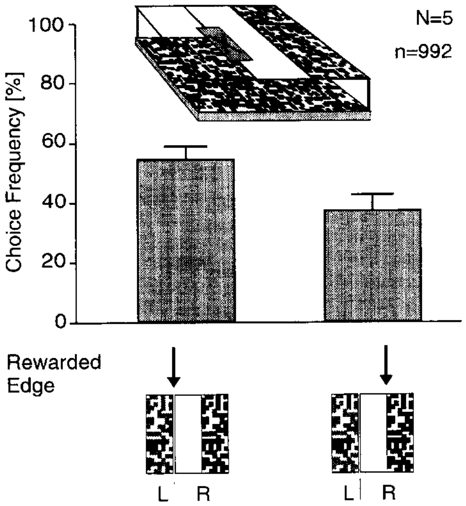

FIGURE 8. Choice frequencies for the combined edge (cross in inset) after two different training procedures, as indicated by the arrows in the insets below abscissa. During training bees were rewarded at the combined edge (left) or at the texture edge (right). N = number of bees participating in experiment, n = total number of landings that contributed to the displayed results. Note that the statistics have been performed on "N" rather than "n". Height difference between raised (R) patterns and low (L) platform was 3 cm. Bees landed significantly more often at the combined edge when the combined edge rather than the texture edge was rewarded during training (Mann–Whitney U-test, $U_s = 23$, $P < 0.05$).

dence between the results of the simulations and the experiments suggests that edge detection by the bee can be explained by a single edge detection mechanism sensitive to both motion and texture cues and organized roughly as illustrated in Fig. 4. We do not mean to imply, however, that the boundaries of objects might not be detected by other kinds of edge detection mechanisms in tasks other than detecting and landing on edges. There is, for example, no evidence that the postulated network, mediating the detection of edges seen in the ventral visual field, is involved also in the recognition of the orientation of edges and patterns the images of which are stationary on the frontal or lateral retina (e.g., van Hateren *et al.*, 1990; Srinivasan *et al.*, 1993; Zhang & Srinivasan, 1993).

The conclusion of a single edge detection mechanism is based on the following results: (i) In accordance with the findings of earlier work (Lehrer *et al.*, 1990; Srinivasan *et al.*, 1990) bees can use texture and motion cues to detect edges. Accordingly, the model edge detection mechanism responds to edges defined by texture and motion cues. (ii) The combination of texture and motion cues does not increase and might even decrease the detectability of an edge, when compared with the detectability of edges defined by the cues in isolation. This finding indicates an apparent antagonistic interference of these cues in the edge detection mechanism. It is the most astonishing finding of our behavioural experiments, since it is in stark contrast to the naïve expectation that two cues are better than one. The performance of the model is in accordance with these experimental results. (iii) Bees, when landing, prefer to face the raised side of a relative motion edge and the textured side of a texture edge. Both of these results are in accordance with earlier findings (Srinivasan *et al.*, 1990; Lehrer & Srinivasan, 1993). The distribution of landing directions recorded at the combined edge is less extreme than that recorded at the other two edges. Nevertheless, at a height difference of 5 cm between the raised homogeneously black or white square and the randomly textured platform, bees preferred to face the raised side of this edge. For the experiments with the white square this again corresponds well to earlier findings: about 70% of the landings of trained bees faced the inside of a raised homogeneously white square that was centred 5 cm above a randomly textured background (Lehrer & Srinivasan, 1993). The detectability of either edge by the model mechanism with respect to the direction of approach corresponds well to the respective distribution of landing directions of real bees at the particular edge.

The importance of brightness differences

As indicated in the *Materials and methods* section, the two surfaces flanking a texture edge differ not only in their textural properties but also in their mean brightnesses. Brightness differences can be used by the bee to detect a boundary [Fig. 3(c); Lehrer *et al.*, 1990]. Hence, this additional cue might have contributed to the detection of the texture edge. The brightness gradient, however, seems to be only of minor importance for the edge detection performance of the landing honeybee. This is indicated by the fact that bees landing at the texture edge are oriented towards the textured side irrespective of whether the homogeneous side is black or white, i.e., irrespective of the actual brightness gradient [Fig. 3(c)]. In addition, the choice frequencies for the two texture edges presented in the respective experiments are larger than the choice frequencies of the corresponding brightness edges (data not shown), also indicating that it is the texture cue rather than the brightness cue that is of major importance.

Plausibility of the proposed model

In our model of edge detection by the bee, motion and textural information from two adjacent patches in the visual field is sensed by two-dimensional fields of correlation-type movement detectors. Separate On and Off motion detectors subserve each patch. The output of all detectors subserving either patch is pooled by integrating cells and the signals of these two cells are compared at a subtraction stage. The resulting signal is then rectified and forms the output signal of the model. The rectification can be interpreted as the dissimilar treatment of positive and negative signals by neuronal mechanisms, which is not implausible.

Our model simulations were intended to demonstrate that a single edge detection mechanism is sufficient to explain major characteristics of the edge detection behaviour of the bee rather than to prove a specific layout. Moreover, implementing separate On and Off motion detectors allowed us to differently weight brightness changes with opposite polarity without much effort in order to cope with the observed asymmetries in the visual system with respect to the processing of brightness increments and decrements, respectively. Other solutions to account for these asymmetries might work as well, such as in the detector input channels, as has been suggested for the fly visual system (Egelhaaf & Borst, 1992).

Two features of the model are very critical to the output and will be discussed in greater detail below: the implementation of the correlation-type movement detector and the size of the receptive field of the integrating cells.

The movement detectors

We have implemented the correlation-type movement detector as a motion and texture sensitive input element to the model edge detection mechanism. The correlation-type movement detector has been demonstrated to be sufficient to explain major characteristics of many optomotor systems, found in insects, crustaceans and vertebrates (for review, see Borst & Egelhaaf, 1993). Moreover, motion sensitive visual interneurons of several insect species can be described by this type of movement detector (for review, see Egelhaaf & Borst, 1993). Most important, neurons with this feature have been found also in the optomotor system of the bee (Ibbotson, 1991).

The optomotor response of the bee has been demonstrated to be colour-blind (for review, see Kaiser, 1975) as are various other behaviours like movement avoidance behaviour (Srinivasan & Lehrer, 1984), scanning behaviour (Lehrer *et al.*, 1985), distance discrimination (Lehrer *et al.*, 1988), and figure–ground discrimination through relative motion cues (Zhang *et al.*, 1995). All these behaviours clearly rely on motion information and are driven by signals from the green receptors only. If the motion detectors underlying the optomotor response are also involved in the edge detection mechanism, edge detection by the bee should be colour-blind as well and driven by the green receptors only, as has indeed been demonstrated in earlier studies (Lehrer *et al.*, 1990). When an object differs from its background in colour, bees only land selectively on the boundaries of the object if the difference in colour provides contrast to the green-sensitive photoreceptors. Otherwise they land everywhere within the object rather than exclusively at its boundaries. Colour blindness of both optomotor response and edge detection is consistent with our hypothesis that both behaviours are mediated by the same type of movement detectors.

The output of the correlation-type movement detector depends not only upon the velocity of the stimulus, but also on its textural properties (for review, see Egelhaaf & Borst, 1993). Nevertheless, not every textural difference within the stimulus leads to a distinct edge response of the model edge detection mechanism. We tested whether the edge detection mechanism responds to an edge defined exclusively by factor 4 differences in the pixel size of the pattern elements on either side of the edge. The model output does not indicate the presence of such an edge (data not shown). Since the size of the larger (smaller) pixels was chosen to be identical to the size of the pixels of the raised (lower) surface of the relative motion edge, these simulations also indicate that the detection of the relative motion edge by the model is due to relative motion—and not to differences in apparent pixel size. Interestingly, real bees are not able to detect a randomly textured object with pixel elements three times larger than those of its randomly textured background, as long as there is no relative motion between object and background (Srinivasan *et al.*, 1990).

Receptive field size of integrating cells

The receptive field size of the integrating cells is important for the performance of the model. Even though we did not systematically investigate this point we, nevertheless, concluded that the receptive fields have to be rather large in order to mediate reliable edge detection. Large receptive fields are especially important for the detection of the relative motion edge flanked by two randomly textured areas, one raised above the other. For instance, at a flight altitude of 1 cm above the raised perspex, which corresponds to the frequently observed low altitude of bees when searching for edges (Srinivasan *et al.*, 1990), a single pixel in the raised surface subtends an angular size of 16.7 deg at the eye of the model bee. Thus, the integrating cells need to have large receptive fields in order to span more than just a few pixels. Only then can the model response to the relative motion edge be significantly larger—depending on flight direction and flight velocity—than the responses to the edges of the individual pixels (Fig. 6). From the occasional presence of the latter responses we can predict that real bees will land not only at the boundary of a relative motion edge, but occasionally also well within the textured areas. This has indeed been observed in earlier studies (Srinivasan *et al.*, 1990; Lehrer & Srinivasan, 1993).

Therefore, we set the size of each of the two integrating cells to 64.5 deg in the x-dimension. The x-dimension reflects the extent of the receptive field perpendicular to the edge. The y-dimension of the receptive field was mimicked by repeating the simulations 200 times. These multiple repetitions smooth out most of the modulations of the model output caused by the edges of the individual pixels. However, repeating the simulation 200 times made the y-dimension of the receptive fields of the integrating cells unrealistically large. In addition, since each repetition was performed with a textured surface defined by a statistically independent sequence, we did not take into account the fact that the pixels of the real random texture covered more than one movement detector, not only in the x- but also in the y-dimension. It is important to note, however, that the results obtained when repeating the simulations 200 times did not differ qualitatively, apart from being somewhat smoother, from those obtained when the number of repetitions was limited to 20.

Relevance of the model

The relevance of the proposed model for the edge detection behaviour of the bee is critically linked to its ability to match important features of the edge detection performance of real bees. With respect to landing direction the model output fits the behavioural data quite well. The way the detectability of either edge depends on the flight direction of the model bee corresponds closely to the distribution of landing directions of real bees at either edge. Of course, the distribution of landing directions at an edge—recorded after landing—does not directly reflect the detectability of the edge while approaching it from either direction. Interestingly, as has been shown by a video analysis (Lehrer & Srinivasan, 1993), bees trained to find a relative motion edge do land much more often when approaching from the lower side than when approaching from the raised side. This finding indicates that real bees do not detect the edges independently of flight direction, which closely corresponds to the performance of our model mechanism. From the results of the simulations we can formulate testable predictions about the consequences of the flight velocity of the bee upon the detectability of different types of edges. For example, bees eventually landing at the texture edge on average should fly faster when approaching the edge than bees eventually landing at the relative motion edge. Or, in other words, slowly flying bees approaching a texture edge and rapidly flying bees approaching a relative motion edge in most cases should cross the respective edge without landing on it. Since we did not video tape the behavioural experiments we lack information on the flight speed of real bees while approaching and detecting an edge. Therefore, these predictions have to be tested in future studies.

The proposed model has been developed in order to explain the behavioural responses of honeybees to the stimuli employed in the behavioural experiments. Therefore, the significance of the edge detection model arises from the behavioural relevance of the visual stimuli employed, i.e., texture and motion cues. Undoubtedly the visual world of honeybees, like the environment of most other animals, can often present objects that differ from their background with respect to textural properties. Therefore, it is likely that the differences are exploited in edge detection. The present and earlier studies (e.g. Lehrer & Srinivasan, 1993) have shown that bees are indeed able to use texture cues to detect object boundaries. The importance of motion cues for bees has been demonstrated in a variety of behaviours (for review, see Lehrer, 1994). With respect to relative motion it is not too speculative to assume that under many circumstances objects, i.e. their boundaries, might be detectable by this cue exclusively, given the environment of flower visiting honeybees. The power of the relative motion cue is stressed by the fact that height differences as small as 1 cm are already suffient to allow the detection of a raised object, as shown in the present and earlier studies (e.g., Srinivasan *et al.*, 1990).

Final conclusions

The most puzzling result of our study is that the combination of texture and relative motion cues can lead to deterioration of edge detection by the bee. This characteristic of the edge detection performance of the bee might be disadvantageous under certain environmental conditions experienced by the bee. We have shown that this characteristic of the edge detection behaviour of the bee can be explained by the assumption of a single edge detection mechanism sensitive to both cues. This neurally parsimonious hypothesis eliminates the need for numerous edge detection mechanisms working in parallel. Therefore, we might speculate that the advantage of detecting edges by a single edge detection mechanism sensitive to several potential cues outweighs the disadvantage of missing edges under certain circumstances. The finding that relative motion is not invariant to texture is important not only in the context of edge detection. It rather might have implications also for distance estimation mediated by motion parallax, for example, which is thought to be an important depth cue in bees (Srinivasan *et al.*, 1989, 1990; Lehrer & Srinivasan, 1993). Further work is necessary to examine the extent to which the perception of object range based on image motion cues depends on the textural properties of the object.

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