ventional myosin is required for the establishment of embryonic polarity. Together with previous analyses implicating microfilaments in generating polarity in *C. elegans*[16,17], our results suggest that actomyosin-based motility is involved in polarizing the zygote.

The interaction between PAR-1 and myosin might directly mediate the asymmetrical localization of PAR-1. The observation that NMY-2 is required for PAR-1 localization is consistent with this hypothesis. However, the finding that NMY-2 is also required to localize PAR-2 and PAR-3 raises the possibility that the role of myosin in localizing PAR-1 might not involve direct binding to PAR-1. Previous analysis has shown that normal PAR-1 localization depends upon functional *par-2* and *par-3* genes, whereas localization of PAR-2 and PAR-3 is not dependent upon *par-1* (ref. 10); L. Boyd *et al.*, manuscript submitted). Therefore, although it is possible that NMY-2 can interact with all three PAR proteins to cause their asymmetrical localization, at present we cannot exclude the possibility that NMY-2 localizes PAR-1 protein indirectly, perhaps through its action on PAR-2 or PAR-3. It is possible, therefore, that the interaction between PAR-1 and NMY-2 contributes to PAR-1 or NMY-2 function in some way other than localization of the PAR-1 protein. For example, PAR-1 might modify NMY-2, perhaps by phosphorylation, to allow localization of the germline-specific P granules to the posterior of the embryo. Experiments specifically blocking the binding of PAR-1 and NMY-2 *in vivo* are needed to determine the significance of this interaction.

Both the actin cytoskeleton and kinases are known to be involved in establishing cell polarity in yeast and mammalian epithelial cells[18]. Our results, combined with analysis showing that conventional myosin heavy chain contributes to cell polarity in *Dictyostelium*[14], and the recent demonstration that an unconventional myosin is involved in asymmetrical cell division in yeast[19,20], suggest that the actin-based motor myosin might be widely used in generating cellular asymmetry. □

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CORRESPONDENCE and requests for materials should be addressed to K.J.K. (e-mail: kjk1@cornell.edu). The *nmy-2* gene sequence has been deposited in the Genbank database, accession number U49263.

Symmetry perception in an insect

Martin Giurfa, Birgit Eichmann & Randolf Menzel

Institut für Neurobiologie, Freie Universität Berlin, Königin-Luise-Strasse 28/30, 14195 Berlin, Germany

SYMMETRICAL **visual patterns have a salient status in human perception, as evinced by their prevalent occurrence in art[1], and also in animal perception, where they may be an indicator of phenotypic and genotypic quality[2–4]. Symmetry perception has been demonstrated in humans[5–8], birds[9–11], dolphins[12] and apes[13]. Here we show that bees trained to discriminate bilaterally symmetrical from non-symmetrical patterns learn the task and transfer it appropriately to novel stimuli, thus demonstrating a capacity to detect and generalize symmetry or asymmetry. We conclude that bees, and possibly flower-visiting insects in general, can acquire a generalized preference towards symmetrical or, alternatively, asymmetrical patterns depending on experience, and that symmetry detection is preformed or can be learned as a perceptual category by insects, because it can be extracted as an independent visual pattern feature. Bees show a predisposition for learning and generalizing symmetry because, if trained to it, they choose it more frequently, come closer to and hover longer in front of the novel symmetrical stimuli than the bees trained for asymmetry do for the novel asymmetrical stimuli. Thus, even organisms with comparatively small nervous systems can generalize about symmetry, and favour symmetrical over asymmetrical patterns.**

Our aim was to examine whether bees can be trained to discriminate patterns purely on the basis of their symmetry, without reference to memorized images. The question of symmetry perception is relevant in an ecological and evolutionary context because bees forage on flowers that display remarkable levels of symmetry[14–15]. However, whether pollinators, like the honeybee, can actually be trained to discriminate patterns purely on the basis of their symmetry is an open question. Here we investigate this question using bilaterally symmetrical and asymmetrical patterns. The patterns were presented in the vertical plane so that their appearance was independent of approach direction[16]. Such an arrangement is ecologically relevant because bilaterally symmetrical flowers mostly present themselves vertically, whereas radially symmetrical flowers tend to present themselves horizontally[14].

Our experiment consisted of presenting the bees with a succession of different stimuli that remained constant only in their degree of symmetry. To test whether the insects were capable of extracting this feature, they were presented with novel stimuli that could be distinguished only on the basis of their symmetry. If the bees selectively choose the novel stimuli displaying the rewarded feature, it is possible to affirm that they can abstract the critical information and transfer it to new patterns. Such a design has been used successfully with pigeons[10] and dolphins[12] trained to distinguish symmetrical and asymmetrical patterns, and with honeybees[17] trained to distinguish pattern orientation.

Single, individually marked, free-flying honeybees were trained to forage on a vertically arranged, circular patch with multiple feeding sites[18] (Fig. 1). The symmetrical group of bees was trained with a succession of eight diverse triads, each consisting of a rewarded symmetrical stimulus and two different non-rewarded asymmetric stimuli presented simultaneously. The asymmetrical group was similarly trained, but with the asymmetrical stimulus

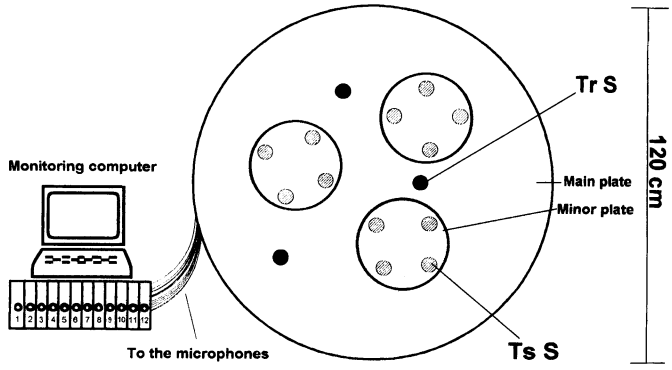
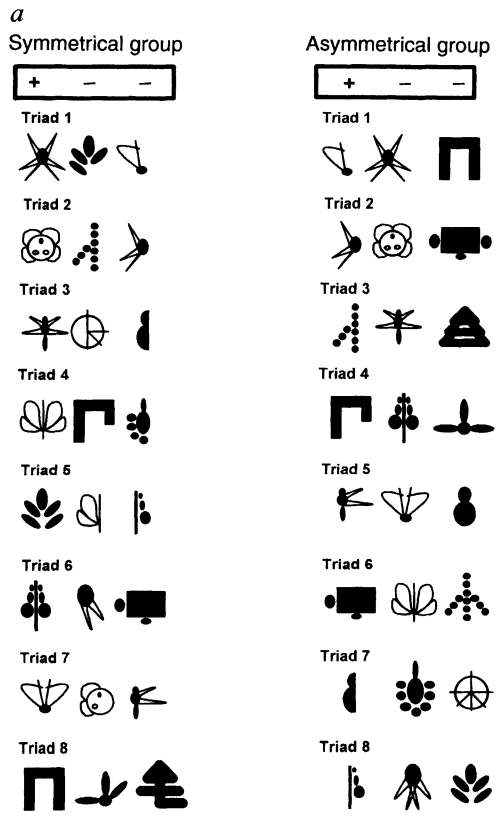


FIG. 1 A multiple choice arrangement to test the choice performance of a single bee using a set of microphones. The main, vertical, round plate (1.2 m diameter, with its centre 1.5 m above the ground) contained 3 training sites (Tr S: black) and 12 test sites (Ts S: hatched), all 7 cm in diameter. During training, only the 3 training sites were visible on the main plate, but not the 12 test sites, and vice versa during tests. The training sites were at different distances from the centre of the main plate to avoid learning of position cues; the test sites were arranged in three smaller subplates, 30 cm diameter (4 per subplate). Both the main and the smaller plates could be rotated independently. Position of the training stimulus was constantly exchanged and the main plate was always randomly rotated. Positions of the test stimuli were changed by rotating the main as well as the minor plates. Each test site was equipped with a pair of microphones for automatic detection of the approaching bee during tests: frequency and intensity thresholds were adjusted to equalize the sensitivity and to detect the bee's flight noise from a distance of 5 cm. The signals of the microphones were converted from an analogue to a digital signal and monitored by a computer with a time resolution of 11 ms. A signal from a given microphone lasting longer than 33 ms was recorded as a choice. For each test stimulus, the number of choices by the bee, the choice intensity, (inversely proportional to the distance from the stimulus) and the duration of each choice were recorded. Stimuli were covered by Plexiglas disks so that bees could neither directly contact nor scent-mark the patterns used. These disks were always carefully washed.

rewarded and the two symmetrical stimuli unrewarded (Fig. 2*a*). Bees were tested with twelve novel stimuli (Fig. 2*b*) in unrewarded, multiple-choice, generalization tests that were interspersed with triad training.

Care was taken to ensure that pattern parameters other than symmetry were randomized during training, so that symmetry was the critical feature associated with reward (Fig. 3). To this aim, parameters that bees are known to employ when discriminating patterns[16] were quantified. Area, contour length and contour density[19] (the ratio of area to contour length) were measured directly on the patterns, and the visual angle subtended by the main axis of the pattern[20] at the recording point was established. Two-dimensional fast Fourier transform amplitude spectra of the patterns were produced and total power[21] (total energy change



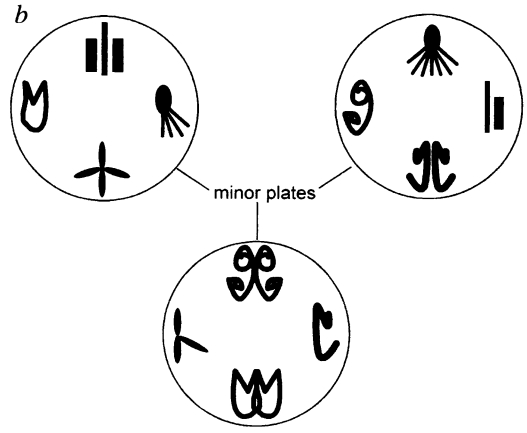
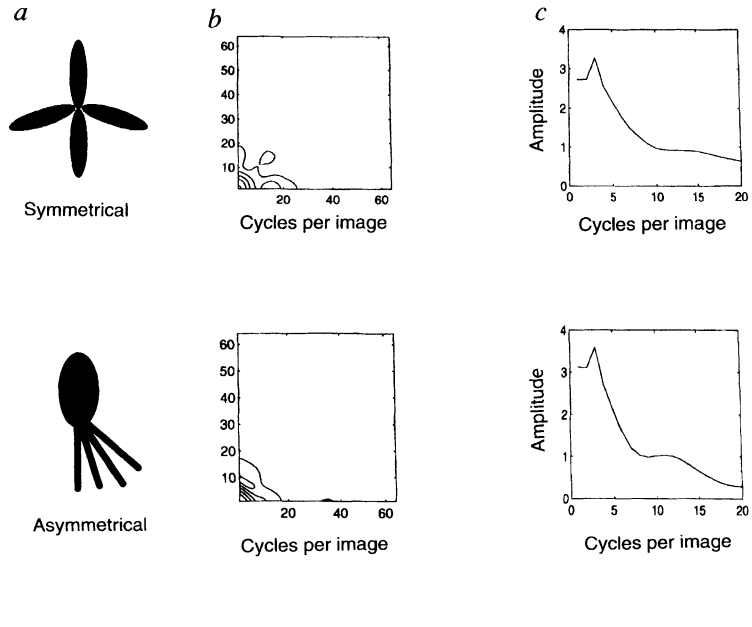


FIG. 2 Training and test stimuli were black and presented against a bee-white background. They were very diverse, except in their symmetrical or asymmetrical outline (see Fig. 3). *a*, Training triads for the symmetrical and the asymmetrical group of bees. +, rewarded stimulus; −, unrewarded stimuli. *b*, Test stimuli arranged on the 3 minor plates. On each plate, two symmetrical and 2 asymmetrical stimuli were presented.
METHODS. Single individually marked, free-flying honeybees were trained with successive triads of stimuli. Two groups of 4–5 bees were established according to the training procedure. The symmetrical group was trained with a succession of 8 triads, each consisting of a rewarded symmetrical stimulus and two different unrewarded asymmetrical stimuli presented simultaneously. The asymmetrical group was similarly trained but with the asymmetrical stimulus rewarded and the two symmetrical stimuli unrewarded. Successive triads were composed of new patterns and did not contain any of the previously trained stimuli. Stimuli forming the training triads were different from those used in tests. Six respective control groups of 3–5 bees (symmetrical and asymmetrical) were run: in two of them, the succession of training triads was randomized with respect to the fixed one (see Fig. 4*d*); in other two, the area of the stimuli was varied by means of a computer program in such a way that all training and test patterns had exactly the same area (6 cm^2), and the succession of training triads was again randomized; in the last two, the visual angle subtended by the patterns at the recording point was varied in such a way that all training and test patterns subtended exactly the same angle (65°). Ten to ninety learning trials per triad were carried out, until a total number of 270 was reached. Training with each triad was interspersed with multiple-choice, generalization tests (a total of 9 tests). During tests, 12 novel test stimuli that remained constant throughout the experiment were presented for 2 min on the test sites. Six were symmetrical and 6 asymmetrical, none was rewarded. For each test stimulus, the number of choices by the bee, the intensity and duration of each choice were recorded.



d

Stimulus	Choice frequency (%) (mean ± s.e.m.) Sym. training (*n* = 21)	Asym. training (*n* = 24)	Contour length	Area	Contour density	Subtended angle	Total power	R.m.s. values H/V	Combined r.m.s. values for Gabor filters s.d. 1	2	4	8
Symmetrical	13.9 ± 1.5	1.4 ± 0.7	26	7	3.7	60	59	1.3	2.3	3.3	2.4	1.6
Asymmetrical	0.4 ± 0.3	7.2 ± 1.3	27	6	4.5	60	61	1.3	3.6	2.1	2.4	1.9

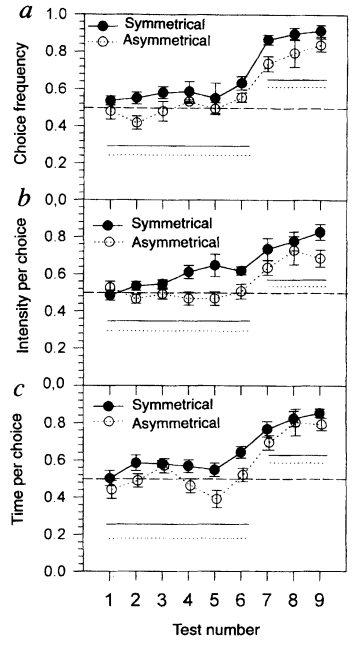
FIG. 3 An example of the analysis performed in the test patterns to check that symmetry was the critical cue allowing discrimination during the generalization tests. Two-dimensional fast Fourier transform amplitude spectra of the patterns were obtained and amplitude spectra were averaged across all orientations. Patterns were convoluted with broad band, highly oriented filters to measure power in the horizontal, vertical and diagonal (positive and negative) orientations. The filters had the form of a gaussian line set in negative circular gaussian which gives zero d.c. Through this analysis, root mean square (r.m.s.) values, a conventional measure of power in signals, were obtained. The vertical filter measures energy in the horizontal axis and gives the horizontal r.m.s. power; the horizontal filter measures energy in the vertical axis and gives the vertical r.m.s. power. Patterns were also convoluted with horizontally and vertically oriented, symmetrical (cos) and asymmetrical (sin) Gabor functions at four spatial scales[23]. The inclusion of these scales is relevant because changes in resolution may affect pattern recognition. The standard deviation (s.d.) of the Gabor gaussian envelope is given in pixels (1, 2, 4 and 8) and the spatial period with which it is multiplied is given by s.d./0.2 (5, 10, 20 and 40 pixels, respectively). Convolutions with symmetrical and asymmetrical Gabor functions were combined to compare horizontal and vertical r.m.s. signal power at the four spatial scales. *a*, A symmetrical and an asymmetrical test pattern. *b*, Two-dimensional fast Fourier transform amplitude spectra of the test patterns; 64 cycles per image equates to 0.5 cycles per pixel. *c*, Amplitude spectra averaged across all orientations. *d*, Choice frequencies of the bees after symmetrical and asymmetrical training, after the generalization performance has been established (test 7 onwards) and the parameters that were considered for pattern analysis: contour length (cm); area (cm^2); contour density[19] (cm^{-1}); angle subtended by the main axis of the pattern[20] at the recording point (°); total power[21]; r.m.s. values for the ratio of horizontal to vertical (H/V) power; and combined symmetrical and asymmetrical r.m.s. values for the vertical/horizontal ratio of Gabor filter orientations at four spatial scales (s.d. 1, 2, 4 and 8)[23]. As shown by this example, there were no marked differences between these patterns, even considering the four different scales employed. When significant differences other than degree of symmetry arose, the bees' responses were examined to test whether such differences accounted for their stimuli choice. In no case could the discrimination of symmetrical and asymmetrical patterns by bees be correlated with differences in a feature other than symmetry.

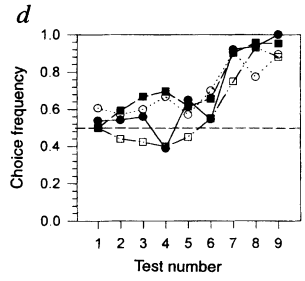
across the pattern) and orientational power were calculated. As bees are especially sensitive to orientation cues[17], orientational power was calculated by convoluting the patterns with broad-band, highly oriented vertical, horizontal and diagonal filters[22], and with symmetrical and asymmetrical, vertically and horizontally oriented Gabor functions[23,24] at four different spatial scales. Such analysis was focused on the test patterns of Fig. 2*b* because these are the stimuli the bees should discriminate as symmetrical and asymmetrical. These analyses did not reveal critical differences between the two classes of patterns other than the degree of symmetry, which would be the reliable cue to distinguish between stimulus categories. When significant differences other than the degree of symmetry arose, the bees' responses were examined to test whether such differences accounted for their stimulus choice. In no cases were the bees' performances correlated with differences in other features.

Bees trained either to the symmetrical or asymmetrical patterns were able to choose consistently the novel symmetrical or asymmetrical patterns, respectively, in generalization tests (Fig. 4). Three measures of performance (choice frequency, choice intensity and choice duration) gave concordant results. A significant deviation from random choices occurred from the seventh test onwards (Fig. 4*a*–*c*), from which point bees preferred to approach the trained feature, came closer to it and inspected it for longer. In all three cases, there were no significant differences between the symmetrical and the asymmetrical group in the first test. Thus, bees did not show 'spontaneous' preferences either for symmetry or asymmetry at the beginning of the test session, and the later preferences were experience dependent. However, for all three parameters, the responses of the symmetrical and the asymmetrical group differed significantly, with the 'symmetrical' bees performing better than the 'asymmetrical' ones. This result demonstrates that bees have a predisposition for learning and extracting symmetry as a feature.

We conclude that honeybees can abstract the cue 'symmetry' and thus generalize it as an image feature. As the abstraction of symmetry made by bees was experience dependent, it was not possible to decide whether it reflected the existence of an innate or a learned symmetry category. 'Symmetrical' bees may have performed better than 'asymmetrical' ones because of an innate predisposition to learn better and faster about stimuli that are biologically relevant[25–26], or because they transferred past experience of predominantly symmetrical flowers in the field. On the other hand, the predisposition for symmetrical patterns is also consistent with the observation that bees spontaneously fly towards symmetrical patterns[27,28] and with the suggestion that symmetry preferences arise as a by-product of the need to recognize objects irrespective of their position and orientation in the visual field[29].

In the training set that we used, bees did not merely learn the symmetry feature, but they generalized it to novel stimuli. This finding clearly differentiates our results from previous ones: although it has been shown that bees may prefer symmetrical





	Triad succession
Bee1	8), 3), 6), 2), 4), 1), 5), 7)
Bee 2	7), 2), 8), 5), 6), 3), 4), 1)
Bee 3	6), 7), 3), 1), 8), 4), 5), 2)
Bee 4	1), 2), 3), 4), 5), 6), 7), 8)

FIG. 4 Choice frequency, intensity and time for both the symmetrical and the asymmetrical group of bees during the successive tests. For each test, these parameters were computed for each stimulus and normalized to 1. The values obtained were added for the 6 symmetrical and the 6 asymmetrical stimuli, respectively. The hatched line at 0.5 indicates no preference for either group of stimuli. Data were analysed by repeated measurements ANOVA, with 'symmetry' as a two-level fixed effect (symmetrical or asymmetrical training). Horizontal lines connect points that do not differ at the 5% level (Newmann–Keuls test); solid line: symmetrical group; dotted line: asymmetrical group. For both groups of bees, there were no significant differences in all three parameters according to whether bees were trained with the fixed or with the randomized succession of triads (repeated measurements ANOVA with 'triad succession' as a two-level fixed effect (fixed or random). Thus, results of both procedures were pooled. Symmetrical group: $n = 1{,}623$ choices (7 bees); asymmetrical group: $n = 1{,}438$ choices (8 bees). Controls where the areas or the subtended angles of both the training and the test stimuli were the same, showed that these parameters did not influence performance (not shown). *a*, The mean relative choice frequency (± s.e.m.) for the trained feature. Bees extracted the symmetry or asymmetry feature and transferred it to the novel stimuli ($F = 34.5$; d.f., 8, 96; $P < 0.0001$) from test 7 onwards. Curves of the symmetrical and the asymmetrical group significantly differ ($F = 7.4$; d.f., 1, 96; $P < 0.02$), with the bees trained for symmetry choosing more frequently the novel symmetrical stimuli than the bees trained for asymmetry did with the novel asymmetric stimuli. The interaction was not significant ($F = 0.3$; d.f., 8, 96; n.s.). *b*, The mean relative intensity per choice (± s.e.m.) for the trained feature. Bees extracted the symmetry or asymmetry feature by coming closer to the trained feature from test 7 onwards ($F = 14.7$; d.f., 8, 96; $P < 0.0001$). The curves significantly differ ($F = 10$; d.f., 1, 96; $P < 0.01$) with the bees hovering closer to the novel symmetrical stimuli when trained for symmetry, than to the asymmetrical ones when trained for asymmetry. The interaction was not significant ($F = 1.5$; d.f., 8, 96; n.s.). *c*, The mean relative time per choice (± s.e.m.) for the trained feature. Bees extracted the symmetry or asymmetry feature by hovering longer at the trained feature from test 7 onwards ($F = 26.1$; d.f., 8, 96; $P < 0.0001$). Moreover, bees hovered significantly longer in front of the symmetrical stimuli when trained for this feature, than in front of the asymmetrical ones when trained for asymmetry ($F = 9.4$; d.f., 1, 96; $P = 0.01$). The interaction was not significant ($F = 0.8$; d.f., 8, 96; n.s.). *d*, Choice frequencies of four different bees rewarded for symmetry. Each bee received a different succession of training triads (right panel: triad numbers refer to those of Fig. 2*b*). Independently of the succession of triads, the bees were capable of extracting the symmetry feature and choosing the new symmetrical patterns, from test 7 onwards.

patterns[27,28], this constitutes the first evidence that they may abstract symmetry as a feature, as a result of their experience. Our results also pose the question of whether bees were categorizing stimuli on the basis of a symmetry concept, raising the possibility that 'cognitive' capabilities may occur in organisms with rather small nervous systems. There may be a simple mechanistic explanation, that central neuronal elements comparing the visual input from the right and the left eye pixel-by-pixel are all that are necessary to perceive the symmetry of shapes. Another attractive explanation is that axes of bilateral symmetry can be found without pattern matching by a local mechanism that identifies edges and lines by classifying relative phases in spatial harmonics[24]. For such a mechanism, an axis of symmetry appears as a line with no contrast. By means of their line and edge detectors[30], insects may perceive no more than the axis itself and thus learn to discriminate patterns on the basis of the axis detectability.

The perception of symmetry is important for pollinators because symmetry of a flower may signal its quality[28], and the reproductive success of plants is affected by the behaviour of pollinators. As pollinators in general may discriminate perceptually between symmetry and asymmetry, they should also be capable of performing selective pollination with respect to floral symmetry[28]. This suggests that plants may have exploited the cognitive capabilities of the pollinators during the evolution of flowers. □

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CORRESPONDENCE and requests for materials should be addressed to M.G. (e-mail: giurfa@neuro.biologie.fu-berlin.de).