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Shape discrimination by wasps (*Paravespula germanica*) at the food source: generalization among various types of contrast

Abstract Wasps (*Paravespula germanica*) were trained and tested at an artificial feeding site, using convex shapes that produced colour contrast, luminance contrast, or motion contrast against the background. With each of the three types of contrast, we tested the wasps' capacity to discriminate the learned shape from novel shapes. In addition, in each experiment we tested the wasps' capability to recognize the learned shape when it offered a different type of contrast than that it had during the training. With the coloured shapes, a side-glance at the colour discrimination performance of the wasps was possible in addition. Wasps are found to discriminate between a variety of convex shapes regardless of the type of contrast that they produce against the background. Mainly, they discriminate the learned shape from novel shapes even if the colour of the shapes or the type of contrast they produce against the background is altered in the test. Thus, wasps generalize the learned shape from one colour to another, as well as between colour contrast, luminance contrast, and motion contrast.

Keywords Colour contrast · Convex shapes · Generalization · Luminance contrast · Motion contrast · Shape discrimination · Wasps *Paravespula germanica*

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Introduction

Due to the anatomical and optical differences between the insects' eye and the mammals', the question concerning the processing of spatial visual information in the insect's brain has always been a challenge. Since the beginning of the last century, studies on insects' shape discrimination using behavioural analyses (reviewed by Wehner 1981, for more recent review articles, see Lehrer 1997) contributed much to our understanding of the mechanisms that are active in learning and using spatial cues in tasks of visual orientation. The insect used most frequently in such studies is the honeybee, which can readily be trained to use artificial visual stimuli for identifying and recognizing a rewarding food source.

Until the mid 1970s, the main cue used by the bee in shape discrimination tasks was considered to be the contrast frequency of the pattern (see for example reviews by von Frisch 1965; Wehner 1981), measured as the quotient between the total length of contours contained in the pattern and the area of the pattern. Later studies demonstrated the use of further cues, such as the distribution of contrasting areas, and the spatial orientation of contours (for references, see Wehner 1981; Dafni et al. 1997).

Very recently, training experiments demonstrated the bees' ability to discriminate among a variety of convex shapes (Campan and Lehrer 2002; Hempel de Ibarra and Giurfa 2003), a performance never reported on in the older studies. In the present study, we use the same shapes used in our studies on the bees to train wasps (*Paravespula germanica*). Some of the experiments are similar to those we have performed on the bees, and some go farther to examine questions that we have not examined in the bee so far.

Convex shapes (also termed closed shapes) are simple geometrical figures, such as a rectangle, a triangle, or a disc, in which every line connecting two points on the circumference of the shape lies within the area of the shape. In the early studies, the bee's failure to discriminate

among convex shapes was explained by the fact that such shapes differ only little in their contrast frequencies (see Hertz 1933). However, based on more recent results (e.g. Wehner 1974; see further references in Wehner 1981), it is much more likely that the true reason lies in the mode of presentation of the shapes. Patterns presented on a horizontal plane can be approached from any direction, so that space-variant parameters such as the orientation and position of edges, or the retinal distribution of contrasting areas, vary continuously and can therefore not be learned. All the results indicating the use of space-variant parameters were obtained using patterns presented on vertical planes.

Regardless of whether an object is presented on a horizontal or a vertical plane, its shape can only be detected if it produces a visible contrast against its background. Each of three different types of contrast renders an object visible: Luminance contrast, colour contrast, and motion contrast. Luminance contrast is perceived when object and background reflect light of the same spectral composition, but differ in the amount of reflected light (i.e. in light intensity). The highest intensity contrast is produced by black objects on a white background (or vice versa). Colour contrast is perceived when object and background differ in the spectral composition of the light that they reflect. Colour contrast is higher; the larger the distance of the loci of the two colours is in the animal's colour space (for references, see Lehrer 1999). An object can produce, at the same time, both colour contrast and luminance contrast against the background, namely when the two differ in both colour and intensity. Shape discrimination in the honeybee was mainly investigated using black shapes on a white background, but from time to time coloured shapes were used as well (e.g., Menzel and Lieke 1983; Ronacher 1992; Lehrer 1999).

Motion contrast is perceived when the object moves relatively to the background. For motion contrast to occur, the background must be patterned, because no relative motion is perceived from an object that moves against a homogenous background. Relative motion is perceived either when a patterned object actually moves, or else when the observer moves in front of an object that is placed at some distance from the patterned background. In the latter case, both the object and the background move at the observer's eye, but the object, because it is nearer, moves faster than the background. The difference between the two velocities constitutes what we call motion contrast (or motion parallax). Bees were found to detect an object the better, the larger is its distance from the background (Srinivasan et al. 1990).

Pure motion contrast is obtained when object and background carry the same pattern. In this case, luminance and colour contrast are absent. The first attempt to train bees to use motion contrast in a shape discrimination task was one in which Zhang and Srinivasan (1994) failed to train bees to discriminate between a patterned ring and a patterned disc presented against a patterned background. Even after a 100 rewards, bees did not learn the discrimination. A second group of bees, however, was successfully trained with the same pair of shapes after the bees had been pre-trained using a black ring and a black disc presented against a white background. The authors explain the success of this two-steps training by arguing that learning a particular spatial cue that is easily detected enhances the learning of the same cue when detection is more difficult. In other words, in the pre-training, bees have learned what to expect. In our own work, using various pairs of convex shapes, we succeeded to train bees with motion-contrast directly, i.e. without any pre-training (Lehrer and Campan 2001; Campan and Lehrer 2002). We found, in addition, that the relevant cue in this discrimination task is situated at the *circumference* of the shapes, a conclusion also drawn by Hempel de Ibarra and Giurfa (2003) and Niggebrügge and Hempel de Ibarra (2003). The failure to train bees directly with motion parallax shapes in the study by Zhang and Srinivasan (1994) might thus be due to the fact that the disc and the ring possess identical outlines.

A special type of motion contrast, whose effect has been examined quite extensively in pigeons (Frost et al. 1990), is produced when a homogenous object moves against a patterned background. In this case, only the contours of the object move relatively to the background, the leading contours covering the pattern, the trailing contours uncovering it. This type of relative motion may be accompanied by luminance contrast or colour contrast, because the homogenous object may differ in colour or intensity from the patterned background.

In our earlier experiments on discrimination of convex shapes in bees, using black-and-white shapes, luminance contrast and motion contrast were considered (Campan and Lehrer 2002). In a more recent preliminary study investigating generalization performance (Campan and Lehrer 2003), generalisation from motion contrast to colour contrast, but not vice versa, was examined in addition. In our present experiments on wasps, we use pairs of shapes that allow us to examine whether or not wasps can use each of the four types of contrast, luminance, colour, and motion contrast, as well as covering parallax, for accomplishing shape discrimination. Training with coloured shapes allows us to look, in additon, at the wasp's colour discrimination performance. Mainly, by presenting wasps trained on one type of contrast with shapes defined by another type of contrast, we examine the wasps' capacity to transfer shape information reciprocally among the different types of contrast.

Material and methods

The study was conducted in the summer of 2003 in a private garden in a suburb of Zurich. A small dish containing sucrose solution was placed on a low table about 3 m away from the experimental apparatus,

attracting foraging wasps searching in the neighbourhood. From this feeding dish, which was permanently present throughout the experiments, wasps were trained to enter the experimental apparatus as described below. Wasps (*P. germanica*) came from a colony whose exact location was unknown to us, but it must have been rather near because wasps kept returning to the apparatus every 2–3 min.

The experimental apparatus

The experimental apparatus (Fig. 1) was similar to that used in our earlier study on the honeybees (Campan and Lehrer 2002). It was placed outdoors under a roof, thus being protected from rain and direct sunshine. The front wall of the apparatus faced north, which was the direction from which the wasps arrived. Depending on the experiment, the front wall, the sidewalls and the floor of the apparatus were covered either by homogenous white paper, or by white paper on which a black random-pixel pattern was printed. The white paper had a flat spectral reflection (see Fig. 2 in Lehrer and Bischof 1995), i.e. it was bee-white.
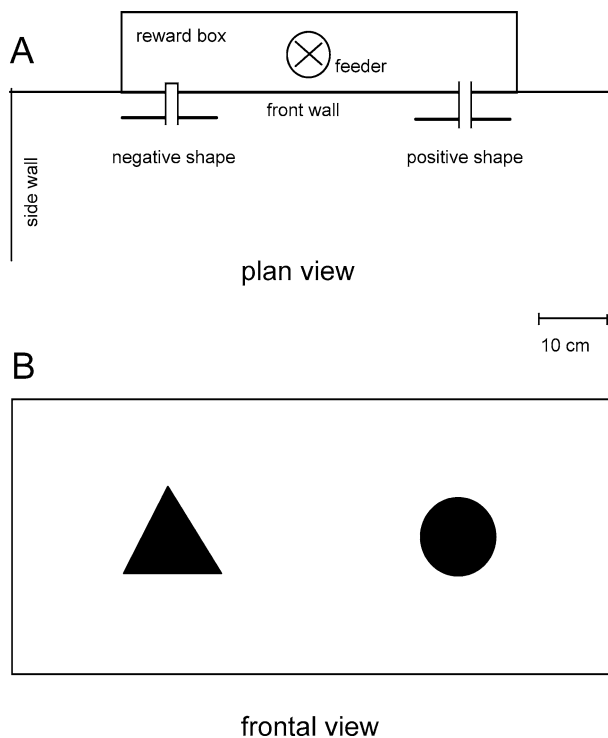
Fig. 1a,b The experimental apparatus. **a** Plan view, **b** frontal view. Two shapes, one rewarding (termed positive), the other not (negative), are presented simultaneously, each mounted on a 50-mm-long Plexiglas tube that penetrates its centre and connects the front wall of the apparatus with the reward box affixed behind it. The tube associated with the positive shape is open, whereas the tube leading through the alternative shape is blocked at its far end by a piece of black cardboard. After training wasps with a particular pair of shapes, they are tested by offering them a choice between the positive shape and each of several novel shapes, or between various pairs of shapes that are all novel to the wasps
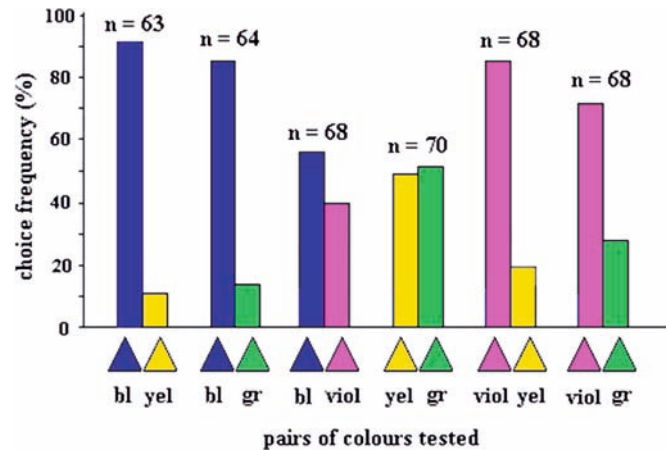
Fig. 2 Results of colour discrimination tests. Wasps trained with a *blue square* (positive) versus a *yellow square* (negative) are tested with various pairs of *coloured triangles* (abscissa) as specified. The bars (*coloured*) accordingly, denote choice frequencies (CFs) in favour of each of the two colours. *n* denote the total number of choices recorded with each pair

Two Plexiglas tubes, 40 cm apart, 18 mm in diameter, were inserted in the front wall of the apparatus, connecting it with a dark reward box affixed behind the wall. The tubes were 60 mm long, so that after having inserted their ends in the reward box they protruded by 50 mm out of the front wall. The shapes to be used in the experiments (see next section) were mounted on the front end of each tube and thus at a distance of 50 mm from the front wall, that served as background.

Wasps could enter the reward box only through one of the two tubes at a time, because the other tube was blocked by a piece of black cardboard affixed behind its far end. The wasps could land on each tube and creep through it, but if they chose the blind tube they had to creep back and try again.

Throughout each experiment, two shapes were presented to the wasps simultaneously (see Fig. 1). One, termed positive, was mounted on the front end of the open tube, the other (negative) on the plugged tube. The two shapes interchanged their places after every two to three rewarded visits (on the average of all wasps), to prevent the wasps from developing a preference for the right or left tube. The black cardboard blocking the far end of the negative tube was moved as well, so that the negative shape never allowed access to the reward.

The visual stimuli

Five different shapes were used: a disc, a square, a diamond, a triangle with its vertex pointing upwards, and a triangle with the vertex pointing downwards. The square and the diamond, as well as the two triangles, were identical, except for their spatial orientation: The diamond was rotated by 90° as compared with the square, and one triangle was rotated by 180° as compared with the other one (see insets in the illustrations). Each shape was cut out of black cardboard covered by one of four

different papers, thus making four different sets of shapes: blue, yellow, black, and a black-and-white random-pixel pattern. A suitably sized hole in the centre of each shape allowed mounting it on one of the tubes.

Although the distance between shapes and background was only needed for producing motion contrast (see Introduction), we kept this distance constant throughout all the experiments, even when only colour or luminance contrast was used. This measure gave us the option of switching from luminance contrast or colour contrast to motion contrast, and vice versa, without confusing the wasps by suddenly introducing a new situation in the test.

Initiating a training experiment

Bees departing from a novel food source display the so-called "turn-back-and-look" (TBL) behaviour, turning around to look at the food source closely before leaving for home (Lehrer1991). It was shown that, during the TBL, bees memorize several cues that enable them to recognize the position and appearance of the food source upon their next visit (Lehrer1993a). Bees passively transported into the reward box usually found its entrance on their first active return. The TBL was exploited ever since to facilitate the training of bees to the experimental apparatus. Soon it was discovered that social wasps (*P. vulgaris*) perform similar TBLs (Collett and Lehrer1993), which now made us try the same procedure on our wasps.

We transported wasps from the permanent feeder, along with the feeding dish, into the dark reward box. For the first experiment, out of about 15 wasps transported passively, 11 returned actively and found the entrance to the tube leading to the reward box. There they were marked as they were feeding. It was impossible, however, to mark each wasp individually, because this required a code of two coloured spots. In contrast to honeybees, which wouldn't move for as long as they are feeding, the wasps kept flying away as soon as one came near. We were therefore content with only one coloured spot, which was sufficient for our purpose, as it allowed to distinguish between trained (marked) and naïve (unmarked) animals. As a result, we were unable to separate wasps that visited the experimental site frequently, and might have therefore learned better, from such that came less often and have therefore learned less. However, from long experience we know that, if the insect is able to accomplish the discrimination, then including the results of several "bad learners" will never lead to the conclusion that it cannot. In other words, our results might be conservative, but not wrong.

Scoring

Typically, within each time interval of 10 min, each wasp visited the apparatus two to three times. On each visit, the wasp's choice between the two shapes was recorded. A choice was defined as entering the tube associated with one of the shapes. A choice in favour of the positive shape scored a plus point, and a choice for the negative shape a minus. On every visit, only the very first choice was recorded, i.e. entering the tube at the positive shape scored a plus only if the wasp had not entered the negative tube before landing on the positive one. This measure was taken in the light of the fact that a wasp that had entered the plugged tube will very soon turn around and hurry to the other (correct) tube. If both the first and the second decision were recorded, then such a wasp would score one minus and one plus point, whereas a wasp that had made a correct choice on its first trial will only score one plus. Thus, the result would be 66.7% for the positive shape even if only half of the wasps' choices were correct.

Our scoring method rendered one plus point or one minus point for each wasp on each of its visits. The next choice of a wasp was the one made on its next visit. Thus, not only the choices of different wasps, but also the choices of each individual wasp were independent of one another. For each test, the proportion of plus points (choice frequency, CF) was calculated from the total number of choices recorded in that test.

Training

The two shapes to be used in the training were mounted on the two tubes prior to each experiment, so the wasps saw them as soon as they performed the first TBL. For quantifying the success of the training, the wasps' choices during the training were recorded from the very beginning of the training. Recording for periods of 10 min every hour on the 1st day, and at least twice every day on the following days, informed us about the level of learning. The final CF in favour of the positive training shape was calculated from all the choices recorded during the training throughout the experiment, with the exception of the 1st hour, which always rendered the poorest result. The CFs thus obtained and the numbers of choices on which they are based are given in the insets of Figs. 3, 4 and 5.

Discrimination tests and transfer tests

In each experiment, the two shapes used during the training were kept constant. Two different types of test were then conducted with the trained wasps. In one, termed discrimination tests, the positive test shape was identical with the positive training shape, whereas the alternative one (the negative test shape) was novel to the wasps. In the other type of test, termed transfer tests, both test shapes differed from the training shapes in either colour or pattern, thus producing a different type of contrast against the background. During the tests, wasps continued to be rewarded. Reinforcement
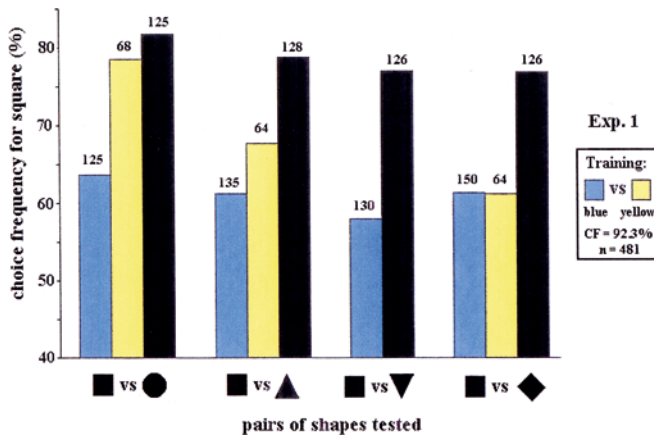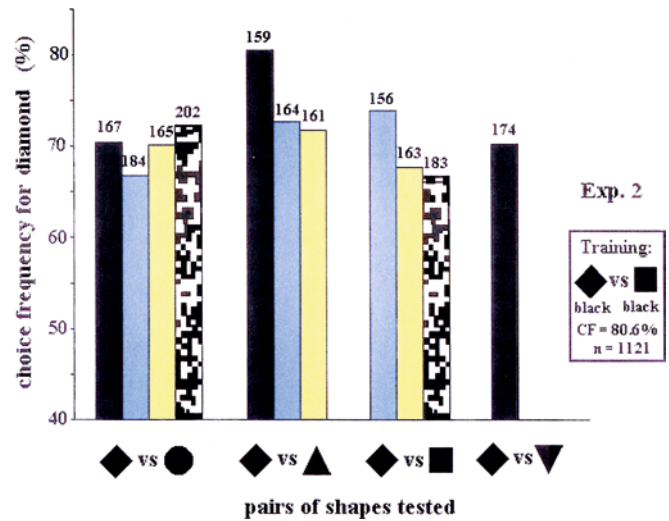
Fig. 3 Results of experiment 1: discrimination of coloured shapes, and generalization between colours. Wasps were trained with the blue square and the yellow square as in Fig. 2. Inset shows the CF obtained during the training and the number of choices (*n*) on which it is based. The trained wasps are then tested by offering them a choice between a square and each of four novel shapes (abscissa). In the tests, the pairs of shapes were *blue*, as was the positive training shape, or *yellow*, as was the negative training shape, or *black*. For each test, the bar showing the CF obtained in favour of the square is coloured according to the colour used for the pair of test shapes involved. The *number* above each bar denotes the total number of choices recorded in the test

Fig. 4 Results of experiment 2: shape discrimination based on luminance contrast, and generalization from luminance contrast to colour contrast and motion contrast. Wasps were trained with a *black diamond* (positive) and a *black square* (negative) placed against a white background, thus producing high luminance contrast. Inset shows the CF obtained during the training and the number of choices (*n*) on which it is based. The trained wasps then had to choose between a diamond and each of several novel shapes as specified on the abscissa. The pairs of test shapes were either *black*, as in the training, or *blue*, or *yellow*, all presented on a white background. In two of the tests, the shapes and the background were randomly patterned. This constellation contains neither colour nor luminance contrast. However, because the shapes were placed 5 cm in front of the background, they produced motion contrast against the background. The bars denoting the CFs obtained in each test are coloured or patterned according to the colour or pattern used for the pair of shapes tested. The number above each bar denotes the total number of choices recorded in the test

during the tests ensures that the insects neither accumulate in the apparatus during the test, nor learn to avoid the apparatus whenever they notice a novel situation. In the discrimination tests, the positive test shape was anyway identical with the positive training shape, meaning that training was actually continued during these tests. In the transfer tests, the reward was offered at the shape that resembled the positive training shape. For example, when the positive training shape was a black diamond, the positive test shape was a diamond as well, but it was blue, yellow, or patterned, depending on the type of contrast to be tested. In earlier studies it has already been demonstrated that short periods of reward on novel shapes do not interfere with the memory of the learned shape even when the test shapes differ much stronger from the training shape than has been the case in the present study (see for example Van Hateren et al. 1990; Srinivasan et al. 1994; Horridge 1997). Even in experiments comprising dozens of tests, results of tests conducted at the end of an experiment proved to be very similar to those obtained with the same shapes at the beginning of the experiment (Campan and Lehrer 2002).

Each test lasted for a total of 10–15 min, the positive and the negative test shapes being presented on one of the tubes for half of the time, and on the other for the other half. After each test, training with the two original training shapes was resumed for at least half an hour.

The discrimination tests and the transfer tests were repeated in the course of the experiment in a quasi-random order, until the total number of choices (*n*) obtained with each pair of test shapes amounted to at least a 100. In only a few cases, *n* was smaller than this, but it was never smaller than 50.

Control tests

Further tests served as controls, conducting two types of control tests. One served to ensure that the wasps' choice behaviour was based on shape recognition, and not on having learnt to discriminate between the open and the plugged tube. In these tests, both the open and the blocked tubes carried a shape identical with the positive training shape. If wasps choose randomly between the two identical shapes, then we may conclude that they cannot tell the open tube from the blocked one.

The second type of control test was conducted whenever wasps behaved as if they generalized the learned shape to novel shapes in the transfer tests. The aim of these tests was to examine whether or not the performance indicates a true generalization performance. In these tests, the shape preferred in the transfer test was presented against the positive training shape. Generalization can only be inferred if the two shapes are discriminated, i.e. if the preferred test shape is indeed novel to the wasps.
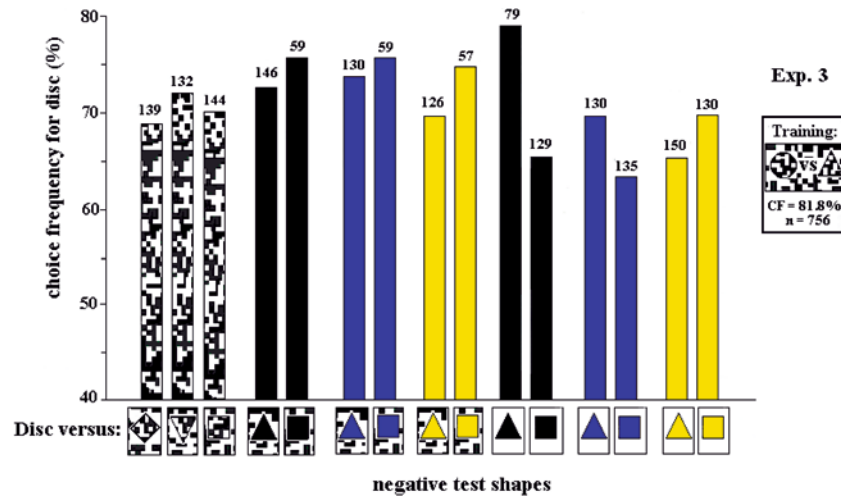
Fig. 5 Results of experiment 3: shape discrimination based on motion contrast, and generalization from motion contrast to luminance contrast and colour contrast. Wasps were trained with a *patterned disc* (positive) and a *patterned triangle* (negative) placed against a similarly patterned background. This combination contains neither colour nor luminance contrast. Due to the distance between shapes and background, however, it produces motion contrast. Inset shows the CF obtained during the training and the number of choices (*n*) on which it is based. The trained wasps were then offered a choice between a disc and other, novel shapes, using seven different combinations of shape and background. In one, the disc and the background were patterned, as in the training, and the alternative shape was one of three novel shapes, a *diamond*, a *triangle*, and as *square* (three bars on the left-hand side). In further tests, the disc was homogonously black, blue or yellow, and was tested against a homogenously black, blue or yellow triangle or square, using, with each pair of shapes, either a patterned or a white background, as specified on the abscissa. The bars denoting the CFs obtained in each test are coloured or patterned according to the colour or pattern used for the pair of shapes tested. Against the white background, the homogenous shapes produced luminance contrast or colour contrast, and against the patterned background they produced, in addition, covering parallax. The *number* above each bar denotes the total number of choices recorded in the test

The permanent feeding place

No recruiting comparable to that of honeybees was observed in the course of the experiments (see also Beier 1984). Some searching wasps, however, arriving singly, eventually found the permanent feeder. The concentration of the sugar solution offered there was kept much lower than that offered in the reward box, to make the experimental wasps take the trouble to creep through the tube. The trained wasps switched to the permanent feeder only when the experiment was interrupted, in which case the apparatus was covered with a large dark blanket. Thus, the permanent feeder ensured that wasps were around when the experiment was resumed. The wasps clearly learned the difference in food quality: as soon as the apparatus was given free again, they left the permanent feeder in great hurry and rushed at the tube entrances.

An experiment lasted for several days, during which several new wasps have found the permanent feeder.

Thus, the feeder kept newcomer wasps away from the experiment. The wasps accumulating there were eventually passively transferred to the reward box as described above, to take part in a new experiment. However, three to five wasps left from the old experiment were allowed to participate in the new one. This meant re-training those wasps, which turned out to be very easy. Indeed, in natural conditions re-learning occurs regularly as different flower species bloom in succession in the course of the season.

The experiments conducted

Experiment 1: colour contrast; training with a pair of figures that differ in colour, but not in shape

In this experiment wasps were trained using a blue square (positive) and a yellow square (negative), presented against a white background. This training situation encouraged the wasps to learn to discriminate the colours, because the two shapes differed in no other parameter. However, during training the wasps had the option of learning, in addition, the shape of the rewarded figure. The trained wasps were then tested for their colour discrimination performance by giving them a choice between different pairs of colours, and for their shape discrimination performance by giving them a choice between the learned figure and each of four figures that differed from it in shape. The pairs of shapes presented in the tests were either blue, which was the positive training colour, or yellow, which was the negative training colour, or black.

Experiment 2: luminance contrast; training with a pair of figures that differ in shape, but not in colour

In this experiment, wasps were trained using two different black shapes, a diamond (positive) and a square (negative), presented against a white background. This training procedure encouraged wasps to learn the difference in shape between the two figures. The aim of this experiment was to see whether or not this procedure rendered a better shape discrimination performance than the previous one, and whether or not the wasps can

transfer the memory of the learned shape to coloured shapes, or to patterned shapes that can only be perceived by using motion contrast (see Introduction).

Experiment 3: motion contrast; training with a pair of shapes that produce motion contrast against their background

In this experiment, the training shapes, this time a disc (positive) and a square (negative), carried a black-and-white random pattern, and so did the background. The distance of 50 mm between the shapes and background ensured that wasps perceived relative motion between the figures and the background. Intensity contrast and colour contrast are absent in this constellation. The aim of the experiment was to examine the use of motion contrast in the shape discrimination task, and to see whether shape generalization also works in the opposite direction to that examined in experiment 2, namely, from using motion contrast during training to using luminance or colour contrast in the tests. In this experiment, the role of covering parallax (see Introduction) was examined as well.

Statistics

Due to the circumstance that wasps were not marked individually, interindividual variations could not be worked out. Another difficulty arises when selecting an appropriate statistical test for the significance of differences between the results of different tests (see Thomson and Chittka 2001). For example, whereas the choices of different wasps are independent of one another, the choices of each individual wasp might be not. In the present study, however, as in many earlier ones (e.g. Srinivasan et al. 1994; Giurfa et al. 1996; Campan and Lehrer 2002; Hempel de Ibarra and Giurfa 2003), the scoring method counteracted this difficulty by taking only the first choice of each wasp into consideration. Thus, although a wasp made several choices during a test, each choice was independent of the previous one.

Tests for the significance of the differences between the results obtained in the tests and the values expected under random-choice conditions ($P = q = 0.5$) were conducted using the χ^2-test. For comparing between paired results obtained from the same group of wasps in two different test types, the Wilcoxon signed ranks test was used. Throughout, tests for significance of differences were only performed in cases in which the significance or non-significance was not clear at first sight. For example, using the χ^2-test, at the 5% significance level, if $n \geq 100$, then CF ≥ 60 always renders significance against the random-choice expectation.

Results

Do the wasps just avoid the plugged tube?

If wasps could discriminate between the open and the plugged tube, then they would not need to rely on the shapes placed there for choosing the correct entrance. It was therefore very important to test whether trained wasps could tell the two tubes apart.

Towards this aim, eight tests were conducted, four in the course of experiment 2, and four in the course of in experiment 3, in which both tubes, the positive (open) and the negative one (blocked), carried the positive training shape (the black diamond in experiment 2 and the patterned disc in experiment 3). If wasps preferred the shape presented on the open tube, then this would mean that they could see which tube was plugged and learned to avoid it.

The tests conducted in experiment 2 rendered CF = 53.1% ($n = 369$), and those conducted in experiment 3 CF = 52.1 ($n = 252$). Calculating the mean value of the CFs, rather than the final CF from the sums of choices, we obtained, for all eight tests, a mean CF = 52.7%, the standard deviation being SD = 2.6%. The highest value obtained for the open tube was CF = 56.9%, $n = 109$, which does not differ statistically from random choice ($P = 0.15$). We conclude that wasps could not see which of the two tubes was plugged. Therefore, the CFs obtained in the present study represent a quantification of the wasp's discrimination performance between the pairs of shapes tested. Indeed, the differences found among test results obtained using different shapes would not be expected if wasps relied on some cues other than those contained in the shapes.

Experiment 1: colour contrast

Wasps learned to discriminate between the blue and the yellow square not only very well, but, in addition, very fast, resembling results obtained from honeybees in colour learning experiments (see for example Menzel 1967). After only about 3–5 rewarded visits, CF for the blue square was 68%, reaching 96.5% after about 20 rewards. The final CF calculated from all 10 learning tests conducted was 92.3% ($n = 481$).

Because the two training shapes differed only in colour, it is clearly colour discrimination that was used in this task. The good performance in the colour-learning task gave us the opportunity to conduct several colour discrimination tests, the results of which are, however, only of secondary importance in the present study. In these tests (Fig. 2), we eliminated the possible influence of the learned shape by using pairs of coloured triangles, rather than squares. The wasps discriminated a blue triangle from a yellow triangle and from a green one much better than from a violet triangle. Yellow and green were not discriminated, but violet was discriminated well from both yellow and green. Very similar results were obtained in colour discrimination tests with honeybees (see Lehrer 1999). Indeed, the spectral sensitivities of the wasp's three types of photoreceptors are very similar to those found in the honeybee (Peitsch et al. 1992).

However, colour was not the only parameter learned by the wasps in this training, as revealed by testing them using pairs of shapes that did not differ in colour. Three

sets of tests were conducted, using blue, yellow, and black shapes (Fig. 3). Discrimination of the blue square from four different novel blue shapes (a disc, two different triangles and a diamond) (Fig. 3, blue bars), was significant, although the CFs were lower than those obtained in the colour discrimination tests (see blue versus yellow in Fig. 2). Evidently, the effectiveness of the parameter "shape" was reduced due to the fact that in these tests both figures had the learned colour.

Indeed, when colour and shape were placed in competition, testing the wasps with a yellow square (that had the learned shape but the wrong colour) versus a blue triangle (that had the learned colour but the wrong shape), they preferred the blue triangle very significantly (CF = 65.6%, $n = 128$, $P < 0.001$) (not illustrated). This result shows that the colour of the learned figure is weighted stronger than its shape, at least using the training procedure employed in this experiment.

In this test, the blue triangle was mounted on the plugged tube, and the yellow square on the open one. The result therefore provides another piece of evidence that wasps do not discriminate the tubes. Had they learned to avoid the blocked tube, then choices would be in favour of the yellow square.

In transfer tests offering a choice between a yellow square and each of three novel yellow shapes, a disc, a triangle and a diamond, discrimination was, again, much above random level (Fig. 3, yellow bars). We conclude that the trained wasps generalize the shape from one colour to another. This conclusion can only be drawn based on the finding that the wasps discriminate very well between yellow and blue. Had they not, then the preference of the yellow square in the transfer tests could simply be based on confusing it with the learned blue square, rather than on a capacity to generalize the learned shape.

By eliminating the influence of the learned colour, the CFs obtained with the yellow shapes were, in two of the three cases, higher than with the blue shapes. Next, the trained wasps were tested in the absence of both training colours by giving them a choice between various pairs of black shapes. Discrimination was excellent (Fig. 3, black bars), not only supporting the conclusion that wasps have learned the shape of the rewarded figure in addition to its colour, but also showing that they transfer the information extracted from the coloured shapes to achromatic shapes. The higher CFs obtained with the black shapes as compared with the coloured shapes are probably due to the high intensity contrast that the combination black-on-white produces (see also Lehrer and Bischof 1995).

To prove that the preference for the black square indeed constitutes a generalization performance, we again must show that the wasps do not simply confuse the black square that was preferred in the transfer tests with the learned blue square. We therefore offered the wasps a choice between these two shapes. In this test, the wasps strongly preferred the blue square to the black one (CF = 82.6%, $n = 127$) (not illustrated).

Summing up the results of this experiment, we conclude that (1) wasps learn and discriminate colours in a similar way that honeybees do, (2) they learn the shape of the rewarded figure in addition to its colour, (3) wasps generalize the information about the shape of a coloured figure to novel figures that possess a different colour or are black, and (4) colour is a more powerful cue than is shape, which might be based on the training procedure employed in this experiment. Whether or not colour is generally more effective than shape will be examined in the next training experiment (experiment 2) that is specifically aimed at shape learning.

Experiment 2: luminance contrast

Whereas in experiment 1 wasps were trained to discriminate between two figures that differed in colour but not in shape, we now train wasps using a pair of training figures that differ in shape but not in colour. The positive training shape was a black diamond, and the negative one a black square. Wasps learned the discrimination well (CF = 80.6%, eight tests) (Fig. 4, inset), although the learning performance did not reach such a high level as with colour learning (CF = 92.3%, see Fig. 3, inset). This result agrees well with earlier results obtained from honeybees, where shape learning was found to be both slower and poorer than colour learning (see for example Lehrer et al. 1985).

Wasps trained in this experiment discriminated the learned black shape not only from the negative training shape, but also from other black, novel shapes (Fig. 4, black bars). In tests using coloured, rather than black figures, the trained wasps were found to transfer the memory of the learned black shape to either blue (Fig. 4, blue bars) or yellow shapes (Fig. 4, yellow bars).

The wasps were now presented with two situations in which shape and colour were pitted against each other. In one, a blue diamond was tested against a black triangle, and in the other a yellow diamond was tested against a black disc. The coloured figures had the learned shape, whereas the black figures had not. The wasps preferred the black triangle to the blue diamond in the first case (CF = 62.9%, $n = 97$, $P = 0.011$), and the black disc to the yellow diamond in the second (CF = 65.9%, $n = 91$, $P = 0.002$) (not illustrated), showing, again, that the parameter "black", similarly to the parameter "blue" (see experiment 1), is a more powerful parameter than is the shape of the learned figure. In experiment 1, the analogous test rendered a very similar result (CF = 65.6%). Thus, colour is more effective than shape, regardless of whether training is specifically aimed at colour discrimination or at shape discrimination.

Finally, the trained wasps were presented with black-and-white randomly patterned pairs of shapes placed against a similarly patterned background. Intensity contrast and colour contrast are absent in this constellation. However, due to the distance (50 mm) between

the shapes and the background, the flying insect perceives relative motion between the figures and the background.

Discrimination of the patterned shapes (Fig. 4, patterned bars) was as accurate as that of the coloured shapes. Thus, wasps transfer the shape information extracted from luminance contrast to stimuli that lack luminance contrast, but offer motion contrast instead.

Again, generalization can only be deduced if control tests show that the shape that is preferred in the transfer tests is discriminated from the learned training shape. We find that wasps discriminate the black diamond from both the blue diamond (CF = 75.3%, *n* = 170) and the yellow diamond (CF = 75.8%, *n* = 178), and particularly well from the patterned diamond placed against the patterned background (CF = 91%, *n* = 83) (not illustrated).

We conclude from these results that (1) wasps learn the shape of an achromatic stimulus and discriminate it from a series of other novel shapes; (2) colour is a stronger stimulus than is shape, regardless of the training procedure, (3) wasps transfer shape information from achromatic to chromatic stimuli, as well as (4) to shapes that are perceived by using image motion.

Experiment 3: motion contrast

In this experiment, the training shapes, this time a disc (positive) and an upright triangle (negative), as well as the background carried the black-and-white random pattern already used in transfer tests of experiment 2. The aim of the experiment was to examine whether generalization of shape occurs also in the opposite direction, i.e. from shapes learned using motion contrast to shapes that are recognized by using luminance or colour contrast.

As expected from the results of the transfer tests described above (see Fig. 4, patterned bars), wasps learned the discrimination well. The results of the learning tests (nine tests, CF = 81.8%) (Fig. 5, inset) are very similar to those obtained with the black training shapes in experiment 2 (CF = 80.6%, see Fig. 4, inset). Furthermore, the wasps discriminated the learned patterned disc from various novel patterned shapes, all presented against the patterned background (Fig. 5, patterned bars). The results agree well with the results obtained from honeybees (Campan and Lehrer 2002). Thus, wasps seem to extract from motion cues very reliable information on the shape of the target.

The trained wasps were now tested in six different transfer tests, using uniformly black, blue, or yellow shapes presented either on the patterned background, or on a white background. Two tests were performed in each of the six situations, presenting the disc either against the triangle (that was negative in the pair of patterned training shapes), or against a square, that was novel to the wasps.

In all these tests (Fig. 5, black, blue and yellow bars), discrimination was highly significant, showing that wasps transfer the shape information extracted from motion contrast to situations in which, instead of motion contrast, colour contrast or luminance contrast is present.

In the tests with the white background, motion contrast was absent, and thus bees could only use colour or luminance contrast to accomplish the discrimination. Luminance contrast was very much higher with the black shapes than with the coloured ones (see Lehrer and Bischof 1995). Still, the results with the coloured shapes are similar to those with the black shapes, showing that colour contrast is as efficient as luminance contrast in this discrimination task (see also Discussion).

In the tests with the patterned background, wasps could also use covering motion parallax (see Introduction). From the results, however, the role of covering parallax is less clear. On the average of all tests, discrimination of the homogenous shapes (black, blue, and yellow) was better on the patterned background (CF = 74.4%, *n* = 577), where covering/uncovering parallax was present in addition to colour contrast or luminance contrast, than on the white background (CF = 68.6%, *n* = 753), where covering parallax was absent. Statistically, however, this difference is not significant (*P* = 0.078, Wilcoxon signed ranks test). We can, at most, say that, although colour and/or luminance contrast are sufficient in this task, covering parallax might add to the reliability of shape discrimination. Unfortunately, there is no way to produce covering parallax without presenting, at the same time, colour- or luminance contrast.

As in the previous experiments, control tests were conducted to make sure that we deal with a generalization performance. The positive training stimulus (the black-and-white patterned disc on the patterned background) was tested against each of the stimuli that were preferred by the wasps in the transfer tests (not illustrated). The CFs for the training shape were 67.8% against the black disc (*n* = 149), 72.7% against the blue disc (*n* = 66), and 79.4% against the yellow disc (*n* = 63), all on the patterned background, and 69.5% against the black disc on a white background (*n* = 59, *P* = 0.003).

Summing up, from the results of this experiment we conclude that (1) shapes perceived using motion contrast are discriminated at least as well as shapes that produce luminance contrast against their background, (2) wasps generalize the learned shape from motion contrast to colour contrast and luminance contrast, i.e. shape generalization between luminance contrast and motion contrast occurs in both directions, and (3) covering parallax plays a minor though traceable role in the discrimination of shapes that provide colour-contrast and luminance-contrast.

Discussion

So far, only few studies were conducted on social wasps at the feeding site, probably because foraging sites of wasps are rather scattered, and, in contrast to honey-

bees, bumblebees and several butterfly species (Chittka et al. 1999), little is known about flower constancy in wasps. Most of these studies were concerned with colour discrimination (e.g. *P. germanica*: Beier and Menzel 1972, *Dolicohvespula saxonica*: Beier1984, *Polybia occidentalis*: Shafir1996). Studies on shape dicrimination were even scarcer. Beier (1984) presented the shapes on a horizontal plane, and found that wasps, similar to honeybees (see Introduction), discriminate shapes solely on the basis of their degree of disruption. A similar conclusion was drawn by Jander et al. (1970) from experiments on *D. saxonica* conducted at the nest entrance. The present study is the first to test discrimination of convex shapes in a social wasp at the feeding site.

Many experiments on shape-based orientation have, on the other hand, been conducted on homing solitary wasps at the nesting site (e.g. Van Iersel and van den Assem 1964; Zeil 1993a, b; Zeil et al. 1996; Collett and Zeil 1997; for older references, see Table 1 in Fauria and Campan 1998). In parasitoid wasps, discrimination of colours and odours, and sometimes of vibratory cues, was examined at the sites of oviposition in the context of host finding (e.g. Lewis and Takasu1990; Meyhofer and Casas1999; Jervis et al. 1993; Dukas and Duan 2000; Colazza et al. 2000; Fischer et al 2001; Meiners et al. 2003; Olson et al. 2003). The large amount of work performed on parasitic species is not surprising in the light of its possible applicability to pest management. However, even among the many studies on parasitoid wasps, we could find only one experiment that was concerned with shape discrimination (Wäckers and Lewis 1999).

Discrimination of convex shapes

Because, in the early studies, the bee was denied the capacity to discriminate among convex shapes (e.g. vonFrisch 1915; Baumgärtner1928; Hertz 1929, 1930; Zerrahn 1934; Wolf and Zerrahn-Wolf 1935), discrimination among such shapes has not been examined systematically for almost 70 years. Indeed, the main shape parameter taken to be used in shape discrimination tasks, the contrast frequency of the pattern (see Introduction) is not very useful in the discrimination of convex shapes. Nevertheless, the wasp *P. germanica* is already the third insect, following the honeybee *Apis mellifera* and the solitary bee *Megachile rotundata* (Campan and Lehrer 2002), shown to discriminate among convex shapes. The discrimination is based neither on contrast frequency nor on overlapping of contrasting areas (see Campan and Lehrer 2002), but most probably on some cues present at the circumference of the shapes (see also Hempel de Ibarra and Giurfa 2003; Niggebrügge and HempeldeIbarra 2003).

In the honeybee, the role of the circumference in shape discrimination is also evident in some experiments by Horridge (1996), and in recent preliminary experiments by Campan and Lehrer (2003). The failure to train bees to discriminate between a disc and a ring using motion cues (Zhang and Srinivasan 1994, see Introduction) provides further evidence for the significance of the outlines. It was only during the pre-training using black shapes on a white background that bees learned to pay attention to the centre of the shapes, which was the site where the two shapes differed from each other (see also Efler and Ronacher 2000).

A suitable way to examine the role of parameters located at edges would be to look whether or not the insect generalizes from filled shapes to identical outline shapes. A generalization of this type can be inferred from some of the experiments by Ronacher and Duft (1996), using luminance-contrast shapes, and from several preliminary experiments using motion-contrast shapes (Campan and Lehrer 2003), in which bees trained with filled shapes were presented with the outlines of the trained shapes.

The role of colour- and luminance contrast

In the present study, we do not compare the amounts of colour contrasts contained in the various stimuli we used, because we are mainly interested in the generalization performance. We plan, though, a detailed colour analysis in a separate study, examining the wasp's colour discrimination in more detail than has been done in the present study. In the present context it is important that the colours we used produced colour contrast as well as luminance contrast against the achromatic background. Our conclusion that, in the experiments with the coloured shapes, shape discrimination was based on colour contrast, rather than on luminance contrast, is based on the finding that wasps did not perform better with the white background than with the patterned background (see Fig. 5). The shapes produce against the white background a much higher luminance contrast than against the patterned background (see Table 1 in Srinivasan and Lehrer 1984), whereas colour contrast is much above threshold in both cases.

Recently, Hempel de barra and Giurfa (2003) suggested that discrimination of convex shapes is mainly accomplished by receptor-specific (and therefore achromatic) contrast to the long-wave receptor. Because the shapes they used subtended 30° at the bee's eye, this finding is in contrast with earlier results by Giurfa et al. (1997) and by Giurfa and Vorobvev (1998), suggesting that objects larger than 15° are detected exclusively on the basis of colour contrast. According to these authors, it is only when objects are smaller than 15° that the detection of coloured objects is accomplished exclusively by the L-system. It would thus seem that object detection and shape discrimination are two different performances, which makes little sense. In the present study, based on the finding that the results obtained with the yellow shapes do not differ from those obtained with the blue shapes, whether a white or a patterned background is used (see Fig. 5), we doubt the participation of the

achromatic L-contrast in the present shape discrimination task (see also Zhang et al. 1995). Indeed, recent results by Niggebrügge and Hempel de Ibarra (2003) suggest that the achromatic L-system is rather insensitive to contrast contained in large objects, but that its response is strongly enhanced when the amount of the L-contrast is increased substantially.

The use of image motion

Honeybees have been shown to use cues derived from image motion for coping with a variety of visual tasks, such as separation of objects from their background, discrimination between moving and stationary objects, edge detection, and distances estimation, all of which involve the use of 3-D information (for references, see review by Lehrer 1994). The use of motion cues for 3-D orientation has also been found in homing wasps at the nest entrance (Zeil 1993a, b; Zeil et al. 1996), in ground-nesting bees and wasps (Brünnert et al. 1994), in the locust (Wallace 1959; Collett 1978), in the larvae of the praying mantis (Walcher and Kral 1994), and in solitary bees (*Osmia*) orienting to a succession of landmarks at various distances from the nest (Fauria and Campan1998). In this long list of motion-dependent behaviours, the use of motion contrast for shape discrimination by the honeybee and by the solitary bee *Megachile* (Campan and Lehrer 2002) is the most recent discovery. The wasp *P. germanica* is now the third insect shown to use motion contrast for shape discrimination.

The particularly good performance of both bees and wasps in using relative motion for shape discrimination might constitute an adaptation of the flying insect to its visual environment. In natural conditions, objects are hardly ever homogenous, and the background is usually structured as well. The capacity to exploit motion parallax as well as covering parallax for detecting and recognizing objects against their background is therefore bound to be extremely useful to an insect moving within a natural scene.

Generalization among different types of contrast

We speak of generalization when an animal is shown to have extracted a particular feature contained in a learned stimulus and use it for recognizing a stimulus that differs from the learned one in all respects but the memorized feature. In a two-stimuli training procedure like the one used here, generalization is expected to involve the feature by which the rewarding and the non-rewarding stimuli differ. In our experiments, the two training shapes differed either in colour (experiment 1), or in shape (experiments 2 and 3). We have seen, however, that even a parameter that is common to both training shapes can be generalized (see also Ronacher1992), and that generalization can involve more than one feature. Thus, in experiment 1, the wasps learned the

parameter "square", in addition to the parameter "blue", even though both training shapes were squares, and in experiment 2 they learned the parameter "diamond", as well as the parameter "black", although both training shapes were black. There is another example from a study on honeybees using pairs of two-coloured shapes, in which the bees learned not only the two colours contained in the positive shape, but in addition, the orientation of the edge between them, although the positive and the training shapes did not differ in the orientation of that edge (Lehrer 1999).

In the present study, we are mainly concerned with the generalization of shape. In our experiments, wasps were trained with colour contrast (experiment 1), luminance contrast (experiment 2), or motion contrast (experiment 3), and were then presented with other types of contrast. In all these tests, wasps recognize the learned shape. They generalize from coloured shapes to luminance-contrast shapes (Fig. 3) and vice versa (Fig. 4), from luminance-contrast shapes to motion-contrast shapes (Fig. 4) and vice versa (Fig. 5), and from motion-contrast shapes to coloured shapes and to such producing covering parallax (Fig. 5).

These findings are not trivial in the light of several studies suggesting that the different types of contrast are processed in different pathways. In the honeybee, several experiments (reviewed by Lehrer 1993b) revealed that colour, shape and motion are processed in parallel and independently, a conclusion already drawn for human vision from psychophysical tests (Livingstone and Hubel 1987; Shiller and Logothetis1990; Burr et al. 1994; Murray and Plainis 2003) (but see Gegenfurtner and Hawken 1996; Willis and Anderson 2002).

In bees, colour is discriminated regardless of luminance (e.g. Menzel and Backhaus1989; Vorobyev and Brandt 1997), motion vision is colour blind (see review by Lehrer 1994), and under large visual angles, shape detection is colour blind as well (e.g. Giurfa and Vorobvev 1998). The separation of the different channels begins already in the retina, based on the various ways by which the photoreceptor responses are processed. Colour is computed from the proportions of the individual responses of at least two (hymenopterans and humans possess three) spectral types of photoreceptor (for excellent illustrations, see Menzel 1987). Luminance, on the other hand, a parameter that bees learn easily when colour cues are absent (Ronacher 1979; Ronacher and Duft 1996), is perceived either based on the sum of responses of all spectral types of receptor (see for example Menzel and Backhaus 1989), or is derived from the response of only one spectral type of photoreceptor (e.g. Giurfa et al. 1997). In either case, colour information is lost, because, when only one receptor type is involved, or when the responses of all receptor types are summed, the proportions of the responses cannot be computed. And, finally, motion detection requires computing the correlation between the responses of neighbouring receptors, taking the time delay into account (see for example Reichardt 1969;

Franceschini et al. 1989). Because all of the receptors involved in motion detection belong to the same spectral type (in the bee, the green-sensitive one, see review by Lehrer 1994), motion detection is colour blind as well (see excellent discussion in Srinivasan 1985).

The insect's generalization among the different types of contrast suggests that there do exist some interactions among the channels that process, each separately, colour, luminance and motion contrast. Possibly, their outputs converge onto a more central instance where the information on a particular feature, in our case the shape of the stimulus or some elements contained in it, is stored. From there it can be retrieved whenever necessary as some kind of more general information that is independent on the type of contrast by which it has been acquired.

In the honeybee, our preliminary results (Campan and Lehrer 2003) revealed generalization from motion contrast to luminance contrast and to covering parallax. Generalization in the opposite direction, i.e. from luminance contrast to motion contrast, might be inferred from the study by Zhang and Srinivasan (1994) cited in the Introduction. Although the authors offer a different interpretation, their success in training bees to discriminate between two motion-contrast shapes after having pre-trained bees with the same pair of shapes presented with luminance contrast might, at least in part, constitute some type of generalization of the shapes from luminance contrast to motion contrast (see also Zhang et al. 1995). At present, experiments similar to those conducted on the wasp in the present study are in progress on the bee, examining its capacity to reciprocally generalize the various types of contrast (R. Campan and M. Lehrer, unpublished observations).

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