

Learning of Geometry and Features in Bumblebees (*Bombus terrestris*)

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Bumblebees (*Bombus terrestris*) were trained to find one of the four exit holes located in the corners of an enclosed environment with a distinctive geometry (a rectangular cage). Panels located at the corners provided nongeometric, featural cues. Between trials bumblebees were passively disoriented to disable dead reckoning. When tested after removal of the panels, bumblebees reoriented using the residual information provided by the geometry of the cage. When tested after removal of only the two panels located in the two geometrically correct corners (the one with the exit and the diagonally opposite one), bumblebees were not able to use features in corners distant to the goal to reorient themselves. Finally, when geometric and featural cues provided contradictory information, bumblebees showed more reliance on featural cues. A similar outcome was observed when the conflict between geometrical and featural information was determined by first training bumblebees in a rectangular cage with a single wall of a different color used as a feature, and then testing animals with the feature displaced along a different wall. When the feature was close to the goal during training, bumblebees chose the corners with the feature at test, when the feature was far from goal during training, bumblebees chose the corners with the correct geometry at test. These results are similar to those revealed by similar transformational tests carried out in vertebrates relying mainly on vision for spatial orientation, that is, birds and monkeys.

Keywords: geometric module, geometry, spatial reorientation, bumblebees

Animals that are disoriented in an environment with a distinctive geometry (e.g., a rectangular enclosure) have been shown to subsequently reorient in accord with the enclosure's shape, sometimes ignoring odor, color, pattern and other featural cues that distinguished its symmetrical locations (Cheng, 1986; Tommasi, Chiandetti, Pecchia, Sovrano & Vallortigara, 2012). Similar behavior has been observed in many species of vertebrates (i.e., fish: Sovrano, Bisazza, & Vallortigara, 2002, 2003; Vargas, Lopez, Salas, & Thinus-Blanc, 2004; birds: Vallortigara, Zanforlin, & Pasti, 1990; Vallortigara, Pagni, & Sovrano, 2004; Sovrano & Vallortigara, 2006; Kelly, Spetch, & Heth, 1998; mammals: Gouteux, Thinus-Blanc, & Vauclair, 2001).

Recently, evidence that the same abilities would be exhibited by invertebrates has begun to appear. Ants (*Gigantipos destructor*, Wystrach & Beugnon, 2009) and bumblebees (*Bombus terrestris*, Sovrano, Rigosi, & Vallortigara, 2012) have been shown to reorient by geometry in a rectangular environment and may also use

featural information provided by colored walls. Evidence in insects promoted the hypothesis (which has been seminal in spatial navigation studies, e.g., Collett & Collett, 2002) that reorientation may be based on two-dimensional (2D) image-matching.

Image-matching mechanisms can explain the results obtained in rectangular arenas because the geometry of space is implicitly contained in panoramic views and does not require any explicit computation (Stürzl, Cheung, Zeil, & Cheng, 2008). This contrasts with the hypothesis that reorientation would depend on geometric analysis of three-dimensional (3D) layout and the idea of distinct processes for geometry and features (Spelke, 2011). Current evidence for vertebrates shows that in some cases, when animals must assume a fixed view of the environment at the goal location, image-matching mechanisms can account for their spatial reorientation behavior (Pecchia, Gagliardo, & Vallortigara, 2011; Pecchia & Vallortigara, 2010, 2012). However, tests that directly compare the 2D image matching and the 3D spatial layout hypotheses favor the latter (Lee, Spelke, & Vallortigara, 2012). For instance, it has been shown that chicks, like children (Lee & Spelke, 2011), spontaneously reoriented by geometric relationships of subtle 3D terrains, and not by salient 2D brightness contours on surfaces or columns (Lee et al., 2012). It can be reasonably argued, nonetheless, that reorientation in vertebrates and in invertebrates may rely on basically different mechanisms. Unfortunately, data for reorientation processes in invertebrates are at present quite limited. In particular, we lack the huge corpus of data from transformational tests (Cheng, 1986), that provided evidence in vertebrates for the priority of large-scale surfaces in the rectangular environments and the way in which featural information is used in such environments. Here we tried the transformational approach in invertebrates, by training bumblebees in a rectangular enclosure with panels at the corners and then testing them with various transfor-

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mations in the spatial arrangement of panels (panels experiment, Experiment 1). In order to check for the effect of the distance from the goal we also used an entire wall of the cage as a feature (white wall experiment, Experiment 2), training bumblebees with the feature near or far from the goal and then testing them after displacing the feature on another wall. Previous work with bumblebees (Sovrano et al. 2012) compared training with short and long, near and far feature, but without any testing involving transformations (i.e., feature displacement). Thus, Experiment 2 aimed at studying the effects of modifying the geometric relations between the goal and the shape of the environment.

Experiment 1

In Experiment 1 bumblebees were trained to reorient themselves in a rectangular enclosure (providing geometric information) with panels located at the corners (providing featural information). Animals were then tested (a) after removal of the overall set of panels, (b) after removal of the two panels located in the geometrically correct corners, (c) after an affine transformation (that altered the overall arrangements of the panels with respect to the geometry of the enclosure).

Method

Subjects

Thirty-four bumblebees (*Bombus terrestris*) were used, supplied by Bioplanet s.c.a. (Cesena, Italy). They were kept in our laboratories (temperature: 25 °C, natural illumination) and fed daily with pellets of fresh pollen and water mixed with honey. Adult foragers (mean body length: 1.7 cm; mean thorax width: 0.7 cm) were used from five different colonies.

Apparatus

The experimental set up (Figure 1a) was described in detail in Sovrano et al. (2012). It consisted of a rectangular enclosure of green plastic material, 20 cm long and 9.6 cm wide, with 8 cm high walls, covered on top with insect net. In each corner an L-shaped wooden block (2.8 × 2.8 cm at the base, and 4.5 cm high) was inserted through a hole in the net (Figure 1b). An opening in the

block gave access from the inside of the enclosure to an L-shaped corridor (1.5 cm in diameter) through which a bumblebee could pass (the exit of which was not visible from the entrance because of the L-shaped structure of the block). All external exits from the blocks were closed by nets except for one (positive or reinforced) that allowed the animal to leave the enclosure. The testing enclosure was inserted in a larger polyester and vinyl insect rearing tent (60 × 60 × 60 cm; Mega View Science Co., Ltd, Taiwan) where food (fresh pollen) was randomly located in 6–8 spots on the floor, thus providing motivation to the animals to exit the rectangular enclosure in repeated trials. All experiments were video-recorded with a video camera (Sony Handycam dcr-sr87), positioned 20 cm above the tent using a tripod.

Procedure

Bumblebees were given two daily training sessions, each consisting of seven trials, with 40 min of inter-session interval, until learning criterion (60% of total correct choices in a single session) was accomplished. At the end of the first daily training session bumblebees were painted with a water-proof pencil to allow identification. During each trial the bumblebee was placed in the center of the arena using a small opaque container (5.5 cm in diameter and 7 cm high) and the number of entrances into the blocks located in the four corners was recorded until the bumblebee was able to locate the correct exit and fly into the larger tent. A bumblebee was considered to have made a choice when its entire body had gone through the hole in one of the corner blocks (this was checked by direct inspection during the experiments and recorded in the sound track accompanying the video recording for checking of interobserver reliability, which was complete among two different observers, Cohen's kappa equal to 1). In each trial, the maximum time allowed to exit the rectangular enclosure was 20 min, after which the animal was disoriented and given another trial. The disorientation procedure involved placing the animal in a closed, opaque small container, 5.5 cm in diameter and 7 cm high, and gently rotating it 360° both clockwise and anticlockwise several times. When the animal chose the correct corner at the first attempt it was allowed a 10 minute period of reinforcement (during which the bumblebee was free to fly and feed in the larger tent); when the animal was able to choose the correct corner and exit only after attempts at the other corners it was given a shorter period of reinforcement in the larger tent (3 min). From trial to trial the rectangular enclosure was

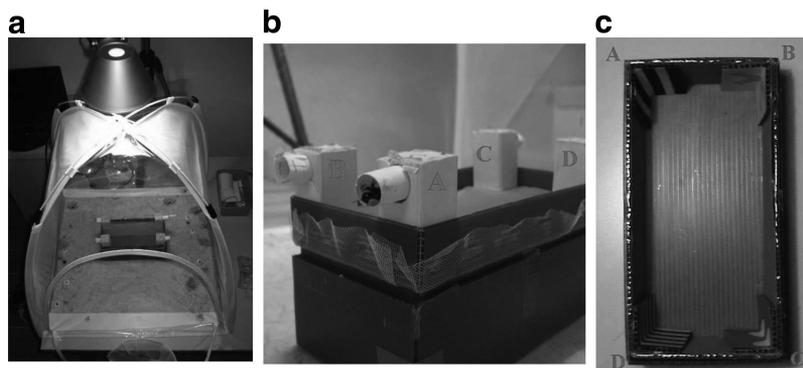


Figure 1. A photograph of the overall set up (Fig. 1a), with details of the L-shaped exits (Fig. 1b) and of the inside of the rectangular enclosure with panels at the corners (Fig. 1c).

rotated 90° clockwise, in order to prevent use of external cues, and, before any trial, the bumblebee underwent the passive disorientation treatment. After the disorientation procedure, the bumblebee was reintroduced to the rectangular enclosure for the subsequent trial. During the intersession interval the bumblebees were kept individually in a tent in the dark to allow identification.

In the experiment with panels, four different cardboard panels ($5.6 \times 8.0 \times 0.2$ cm) were placed in the four corners (see Figure 1c). One panel was a green cross (4.5×4.5 cm) on a white ground; the second panel was a series of four black and three yellow vertical stripes (8 mm each one); the third panel was a series of five blue and five white horizontal stripes of 8 mm; the fourth panel was two white disks (2.1 cm in diameter) on a blue ground (see Figure 1c). Different positive panels (i.e., the one that indicated the corner with the food) were used for different bumblebees; the other three panels were placed in a fixed arrangement for each bumblebee (and in different arrangements for different bumblebee). Training was carried out on 34 animals. At test after learning, bumblebees were tested (a) after removal of the overall set of panels ($N = 10$), (b) after removal of the two panels located in the geometrically correct corners ($N = 12$), (c) after affine transformation (that alters the overall arrangements of the panels with respect to geometry; $N = 12$). The test consisted of a single session of eight trials, in which all openings were closed (extinction procedure); the intertrial interval was 5 minutes, and all other procedural details were the same as in the training phase. We considered for each bumblebee the corner chosen first in each of the eight trials of test. The data were analyzed by analysis of variance (ANOVA) with corners as a within-subjects factors, and distance from feature (near-feature, far-feature) as a between-subjects factor.

Results

In the experiment with panels at the corners, the mean number of trials (with SEM) needed to reach the learning criterion was 16.03 ± 0.53 .

Results of the test with removal of all panels are shown in Figure 2. The analysis of variance revealed a significant heterogeneity associated with corners, $F(3, 27) = 4.900$, $p = .008$, $\eta_p^2 = 0.352$. Bumblebees showed significantly more choices for the two geometrically correct corners, AC vs. BD: $F(1, 9) = 7.309$, $p = .024$, $\eta_p^2 = 0.448$. There was no difference in choice between corners A and C: $F(1, 9) = 0.488$, $p = .522$, $\eta_p^2 = 0.051$ and B and D: $F(1, 9) = 1.161$, $p = .309$, $\eta_p^2 = 0.114$.

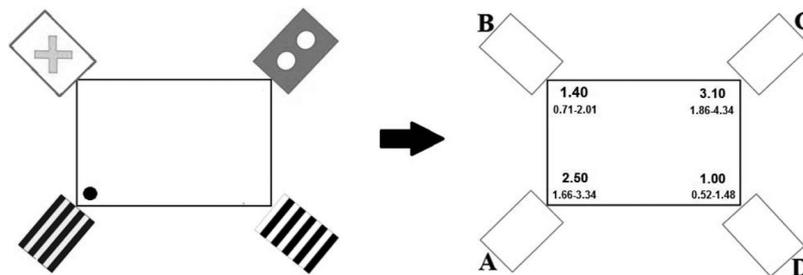


Figure 2. On the right the training condition with the panels is shown (the dot identify the correct exit; actually different animals were trained on different corners as correct, see Methods). On the left, the means (with confidence intervals below) number of first choices made to each corner by the group of bumblebees at test after removal of the panels are shown.

Thus, after learning in the presence of panels in the four corners, when tested after removal of all the panels, bumblebees did not go back to random choices but preferentially chose the two geometrically correct corners. This suggests that the overall arrangements of surfaces was in some way implicitly coded during training, even though local information provided by a single positive panel used as a beacon or by panels used as landmarks sufficed to solve the task during training.

Results of the test with removal of the two geometrically correct panels are shown in Figure 3. The analysis of variance revealed a significant main effect of corners, $F(3, 33) = 18.108$, $p < .0001$, $\eta_p^2 = 0.622$. Bumblebees showed to choose the two geometrically correct locations, AC vs. BD: $F(1, 11) = 36.857$, $p < .0001$, $\eta_p^2 = 0.770$; however, there was no difference in choice between corners A and C: $F(1, 11) = 0.273$, $p = .612$, $\eta_p^2 = 0.024$ and corners B and D: $F(1, 11) = 1.774$, $p = .210$, $\eta_p^2 = 0.139$.

Bumblebees were thus, not able to use the residual featural information provided by panels B and D to discriminate between the two geometrically correct corners A and C. This suggests that information relative to the correct panel was used as beacon and not as landmark. Landmarks are typically conceptualized as distinctive features of an environment that can serve as spatial points of reference; a beacon, in contrast, is a sensory cue that is extremely close to a goal location (or is emanating directly from a goal location) and thus, enables a navigator to travel simply by aiming at it (see Gallistel, 1990). Similar results were reported by Cheng (1986) with rats and Vallortigara, Zanforlin, and Pasti (1990) with chicks.

Results of the test with the affine transformation in the spatial arrangement of panels are shown in Figure 4. The analysis of variance revealed a significant main effect of corners, $F(3, 33) = 7.222$, $p = .001$, $\eta_p^2 = 0.396$. There was no significant heterogeneity associated with choice for corners A, C and D, $F(2, 22) = 0.666$, $p = .524$, $\eta_p^2 = 0.057$. Thus, in the presence of a conflict between geometric and featural information (the correct panel was located in an incorrect geometrical location after the affine transformation), bumblebees seemed to rely exclusively on the featural information provided by the correct panel ignoring geometry.

Experiment 2

In Experiment 1, featural information was provided by panels located at the corners that may act as beacons for reorientation. In

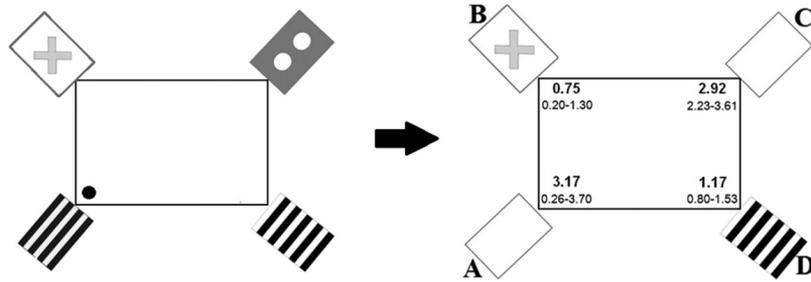


Figure 3. On the right the training condition with the panels is shown (the dot identifies the correct exit; actually different animals were trained on different corners as correct, see Methods). On the left, the means (with confidence intervals below) number of first choices made to each corner by the group of bumblebees at test after removal of the panels in the two geometrically correct locations are shown.

Experiment 2, we used an entire wall of the cage as a feature in order to check for the effect of the distance from the goal in the affine transformation, which modifies the geometric relations between the target and the shape of the environment.

Subjects

Forty-eight naïve bumblebees (*Bombus terrestris*) were used; rearing conditions were the same as in Experiment 1.

Apparatus and Procedure

The apparatus and the general procedure were the same as in the experiment with panels at the corner (Experiment 1); this time, however, one of the walls (either long or short wall, see below) was covered with white cardboard. For half of the animals ($N = 24$) the feature (the white wall) was located near the correct corner (i.e., bumblebees were trained with a green–white corner as positive). For the other half ($N = 24$) the feature was located far from the correct corner (i.e., bumblebees were trained with a green–green corner as positive). Moreover, for half of the animals in each of these groups the feature (white wall) was located on a short wall and for the other half on a long wall. At test, the position of the feature wall was changed (from a long to a short wall for half of the animals and from a short to a long wall for the other half). We considered for each bumblebee the corner chosen first in each of the eight trials of test. The data were analyzed by ANOVA with corners as a within-subjects factors, and distance from feature

(near–feature, far–feature), and type of change (from long to short or vice versa) as between-subjects factors.

Results

In the experiment with the white wall, the analysis of variance on the number of trials needed to reach learning criterion during training revealed that there were no differences associated with using a short or a long wall as featural information, $F(1, 44) = 0.331, p = .568, \eta_p^2 = 0.007$; Means \pm SEM: 16.46 ± 0.88 for long wall and 15.88 ± 0.60 for short wall. There was, on the other hand, an effect of the near versus far position of the feature (the differently colored wall). Bumblebees trained on the corner far from the feature (i.e., a green–green corner) as positive took more trials to criterion than bumblebees trained on the corner near the feature (i.e., a green–white corner) as positive, $F(1, 44) = 6.921, p = .012, \eta_p^2 = 0.136$; Mean \pm SEM: 17.50 ± 0.82 for far-distance conditions vs. 14.83 ± 0.59 for near-distance conditions. There was no interaction between training with short or long wall and distance from feature (near vs. far condition; $F(1, 44) = 0.061, p = .806, \eta_p^2 = 0.001$).

The results of the test with the affine transformation are shown in Figure 5. The analysis of variance revealed a significant main effect of corners, $F(3, 132) = 2.708, p = .048, \eta_p^2 = 0.058$, and significant corners \times type of change, $F(3, 132) = 3.509, p = .017, \eta_p^2 = 0.074$, and corners \times distance from feature, $F(3, 132) = 5.211, p = .002, \eta_p^2 = 0.106$, interactions. There were no other statistically significant effects (type of change, $F(1, 44) = 0.0001$,

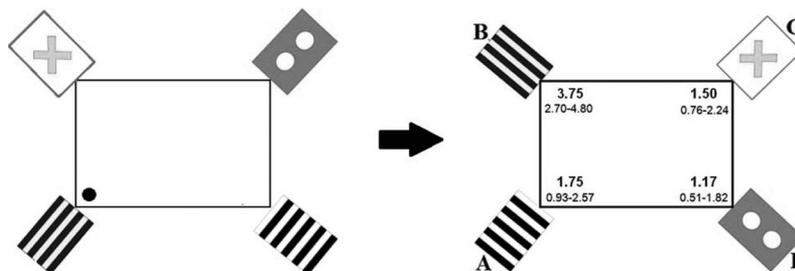


Figure 4. On the right the training condition with the panels is shown (the dot identifies the correct exit; actually different animals were trained on different corners as correct, see Methods). On the left, the means (with confidence intervals below) number of first choices made to each corner by the group of bumblebees at test after the affine transformation are shown.

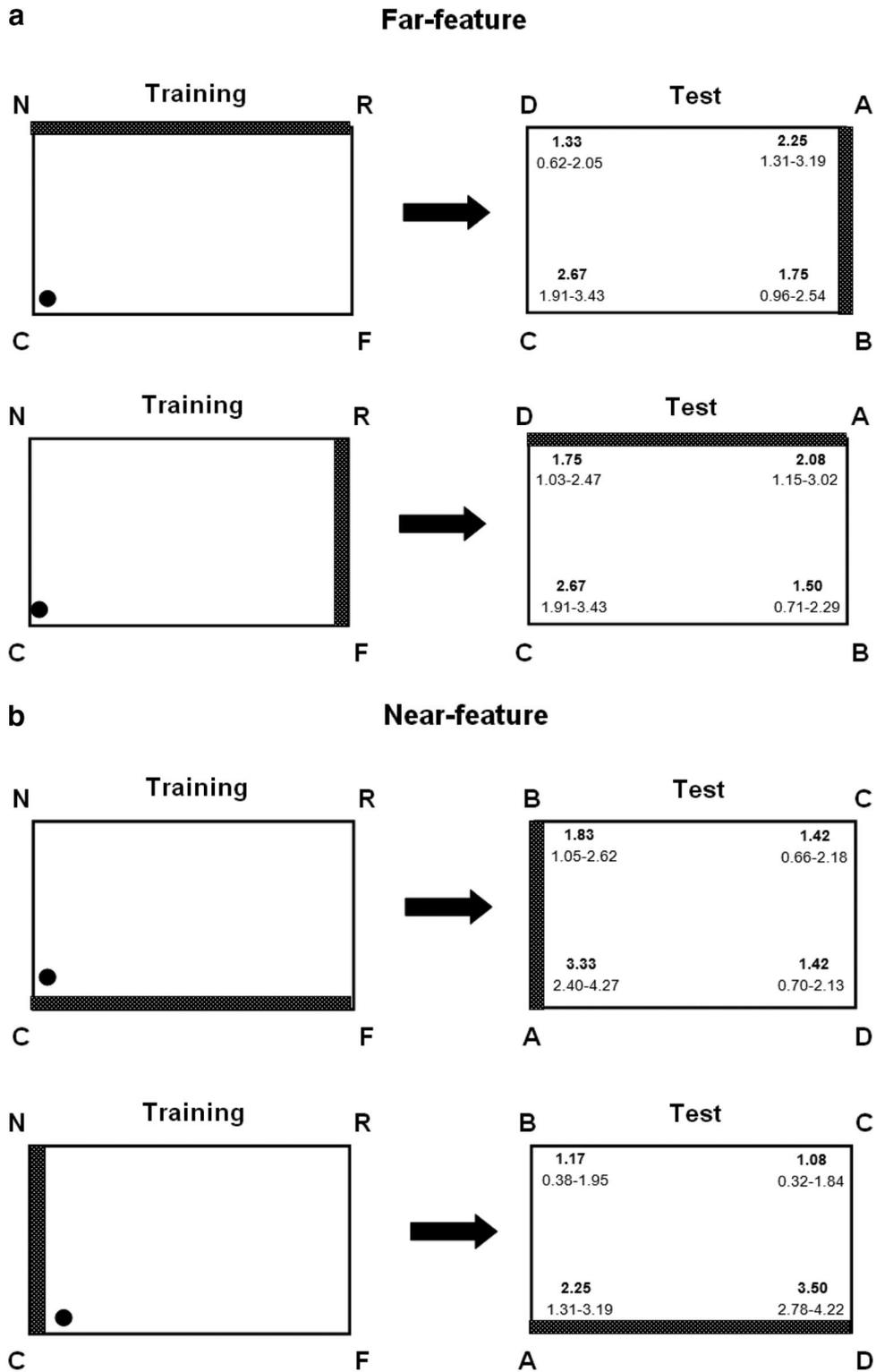


Figure 5. On the right, the training conditions with the feature (the white wall here shown as a gray bar) are shown (the dot identifies the goal, i.e. the correct exit; the feature was either far (Fig. 5a) or close (Fig. 5b) to the goal exit). On the left, the means (with confidence intervals below) number of first choices made to each corner by the group of bumblebees at test after the change in the position of the feature (from long to short, top, and from short to long, bottom) are shown.

$\eta_p^2 < 0.0001$); distance from feature, $F(1, 44) = 0.0001$, $\eta_p^2 < 0.0001$; distance from feature \times type of change $F(1, 44) = 0.0001$, $\eta_p^2 < 0.0001$; corners \times distance from feature \times type of change, $F(3, 132) = 1.563$, $p = .201$, $\eta_p^2 = 0.034$.

Separate analyses revealed that in bumblebees trained in the far-feature condition (green–green corner; Figure 5a) there was no significant effect of the type of change, from long to short wall or vice versa, $F(1, 22) = 0.0001$, $\eta_p^2 < 0.0001$, and no corners \times type of change interaction, $F(3, 66) = 0.202$, $p = .895$, $\eta_p^2 = 0.009$. Overall, there was more choice for the two geometrically correct corners, AC vs. BD: $F(1, 23) = 5.529$, $p = .028$, $\eta_p^2 = 0.194$; no differences were apparent between A and C: $F(1, 23) = 0.986$, $p = .331$, $\eta_p^2 = 0.041$, and between B and D: $F(1, 23) = 0.055$, $p = .817$, $\eta_p^2 = 0.002$.

In bumblebees trained in near-feature (green–white corner) condition (Figure 5b), on the other hand, there was a significant interaction corners \times type of change, $F(3, 66) = 5.103$, $p = .003$, $\eta_p^2 = 0.188$. When the data were considered in terms of choices for the two corners with the landmark (AB in the case of a change from a long to a short wall and AD in the case of a change from a short to a long wall) versus the two corners without any landmark (CD in the case of a change from a long to a short wall and BC in the case of a change from a short to a long wall) a significant main effect of landmark was apparent, $F(1, 22) = 36.321$, $p < .0001$, $\eta_p^2 = 0.623$; the type of change (from long to short or vice versa) and the interaction between landmark versus no landmark \times type of change were not significant, respectively: $F(1, 22) = 0.0001$, $\eta_p^2 < 0.0001$; and $F(1, 22) = 1.453$, $p = .241$, $\eta_p^2 = 0.062$. Separate analyses for the two types of change confirmed the results: from the short to the long feature AD versus BC: $F(1, 11) = 23.435$, $p = .001$, $\eta_p^2 = 0.681$; A vs. D: $F(1, 11) = 2.448$, $p = .146$, $\eta_p^2 = 0.182$; B versus C: $F(1, 11) = 0.030$, $p = .866$, $\eta_p^2 = 0.003$; from the long to the short feature: AB versus CD: $F(1, 11) = 13.146$, $p = .004$, $\eta_p^2 = 0.544$; A versus B: $F(1, 11) = 3.000$, $p = .111$, $\eta_p^2 = 0.214$; C versus D: $F(1, 11) = 0.0001$, $p = 1$, $\eta_p^2 < 0.0001$.

Thus, when the bumblebees were trained with the goal near to the feature (a condition that resembled that used with panels), at test after the transformation they tended to choose the feature and to ignore the geometry (as it occurred in the affine transformations with panels). In contrast, when the bumblebees were trained with the goal far from the feature, at test they tended to choose the geometry and to ignore the feature.

One interesting point is that the two corners with a landmark edge both attracted the bumblebees, to similar extents (Figure 5b). This is puzzling from the point of view of purely matching features because the features in one corner are correct, whereas the features in the other corner are wrong, in that the sense is reversed. However, it could be that having at least the feature elements there (a green color and a white color), plus having the geometry correct might make enough correct to attract the bumblebees there. Averaging the two conditions, this attraction is as high as having all the features correct, but the geometry wrong. This might provide an explanation for the equivalent attraction of the two corners near the landmark on test.

General Discussion

Results of the test after removal of all the panels demonstrate that, as in all vertebrates species studied so far (reviews in Val-

lortigara, 2009) there is (incidental) encoding of geometric information by bumblebees. Even though during training the information provided by panels sufficed to solve the task, results of test when landmarks were removed showed that bumblebees could use the residual information provided by the shape of the environment for a partial disambiguation of the problem. Whether this information is encoded implicitly as part of a panoramic-view strategy (Wystrach, Cheng, Sosa, & Beugnon, 2011) or using explicitly the 3D distribution of surfaces in the terrain (Lee & Spelke, 2011; Lee et al., 2012) remains of course undetermined in the present conditions of testing (but see below for further discussion).

Results also showed that bumblebees could use featural information for reorientation, though uniquely in the form of local sensory guidance cue, not as true landmark. This is revealed by two crucial findings. First, when at test only the panels in the two geometrically correct locations were removed, bumblebees appeared unable to discriminate between them, even though the residual information provided by the remaining two panels would have allowed them to do so. Second, and similarly, when trained with the white wall close to the goal, bumblebees appeared to make use of the feature at test after the transformation; however, when trained with the white wall far from the goal they resumed using only geometry at test, ignoring featural information. All this suggests that bumblebees were using the featural information as a beacon and not as a true landmark.

Comparison with results of transformational tests carried out in other (vertebrate) species suggest basic similarity in behavior, at least with those species that rely mainly on vision. Birds (Vallortigara et al., 2004, 2005), monkeys (Gouteux et al., 2001), and fish (Sovrano et al., 2002, 2003, 2005, 2007; Vargas et al., 2004) all showed to prefer featural information after affine transformation and do not use information from distant panels when tested with removal of the panels in the geometrically correct locations (but see Kelly et al., 1998 for a possible exception in pigeons). Rats, in contrast, committed several rotational errors in reference memory following an affine transformation (Cheng, 1986).

Comparing the present results with those collected in ants (Wystrach et al., 2011) it is worth noting that in the condition with the feature wall far from the target, ants maintained search at the correct location but, differently from bumblebees, did not search at the geometrically equivalent corner. This may be due to attraction to edge by ants which would be modulated also by the size of the feature (previous work by Wystrach & Beugnon, 2009 with smaller features has showed in fact systematic rotational errors).

As noted above, it is doubtful whether these results might prove capable of disentangling the opposite theoretical accounts of reorientation abilities shown by different organisms. On the one hand, given that image-matching is based on the 2D distribution of edges in the scene, changes such as removal of panels would importantly affect this distribution leaving, however, large scale spatial information relatively constant. The fact that tests with removal of the panels revealed use of only geometric information would thus fit in well with the idea that following transformation only large scale information is kept into account by bumblebees. However, it is puzzling in this regard that after an affine transformation, bumblebees clearly chose featural information: One would have expected that they would have relied only on large scale spatial cues, thus choosing the geometrically correct corners. This may appear to be in contrast with use of purely panoramic views;

however, it can be argued that panoramic view is in fact limited to a local snapshot at around the corner (which would account for the discounting of featural information in test with feature far from the goal, i.e., with the white wall far from the exit) and that this predominates over large scale spatial information). In fact pretty much all models of view matching use reference views obtained near the goal (Cheung, Stürzl, Zeil, & Cheng, 2008); thus, in the case of the present experiments the cues at the target corner loom large because the reference view is taken near it.

There is clearly a need to specify better from a theoretical point of view what set of data would be incompatible with either hypotheses, and to test invertebrates under conditions (e.g., Lee et al., 2012) that have proved to disentangle between image-matching and 3D spatial layout hypotheses in vertebrates. Moreover, it should be stressed that predictions based on image-matching hypothesis have to take into account the details of the visual system of the species being tested (e.g., the placement of the eyes). This means that, among other things, image-matching is unlikely to lead to the same behavior on all species, which makes comparisons between vertebrates and invertebrates of particular relevance.

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