International Journal of Comparative Psychology, 2008, **21**, 59-69.

Relative Pattern Preferences by Bumblebees

Catherine M. S. Plowright, Mathieu Lebeau,
and Martine J. Perreault
University of Ottawa, Canada

Bumblebees were trained to discriminate between two patterns, one rewarding (S+) and another unrewarding (S-) consisting of four orthogonal bars. Training and testing conditions were manipulated in a 2 X 2 between groups design. The training patterns differed only in the positioning of the bars in the inferior or the superior portion. The same was true of the testing patterns, both of which were unrewarding. A significant interaction between training and testing conditions was obtained on preference for one pattern, the diamond, which was present at testing for all four conditions. For the groups that were trained with the patterns that differed only in the inferior portion, when tested with patterns that differed in (1) the inferior portion: the diamond, for which the inferior portion matched that of the S+, was chosen at a level significantly above chance (2) the superior portion: the preference for the diamond disappeared--no discrimination was found, even though the alternative to the diamond was the same as the S+. For the groups that were trained with the patterns that differed only in the superior portion, the opposite effect of testing conditions was found: when tested with patterns that differed in (1) the inferior portion: the bees avoided the very same diamond that was preferred by the bees trained differently, and favoured the alternative, which was the same as the S+ (2) the superior portion: no pattern discrimination was found (i.e. the avoidance of the diamond disappeared). Two predictions were disconfirmed: that during testing bees would only (1) approach the pattern that was the same as the S+, or (2) discriminate between patterns that differed in the same area (inferior or superior) as did the training patterns. The data were in line with the interpretation that during differential conditioning the visual field used in future pattern discriminations is expanded to include not only the inferior portion of the pattern but more of the superior portion as well.

This paper addresses a general question in animal cognition as it applies to learning in bumblebees: once a discrimination has been learned, what is it that is remembered and used in future discriminations? In other words, what are the contents of memory? This question has been comparatively neglected in the literature (Dyer, 1998). We have recently addressed this question in the context of spatial learning (Church & Plowright, 2006). Here we consider the case of visual pattern discriminations, which are particularly relevant to the broader question of how invertebrates categorize visual stimuli (Benard, Stach, & Giurfa, 2006).

Three different research strategies in pattern learning can be identified in the literature. (1) The first is to train bees to discriminate between patterns by rewarding approach to one (the positive stimulus, or S+) and not rewarding approach to the other (the negative stimulus, or S-). A learning curve can be traced, and final discrimination performance measured. A rich catalogue has now been assembled of patterns that can and can not be distinguished by honeybees following training (see reviews by Horridge, 1997, 2005, 2007). (2) The second strategy builds on the first: training experience is manipulated and then a common test is given. This method truly assesses learning because group differences on a common test can not be attributed to the current conditions but are traceable to the memories of prior experience (Shettleworth, 1998). As an example, we have recently used this method to show that patterns seem, by and large, undiscriminable on their own (e.g., a square vs. a square

This research was supported by a research grant by the Natural Sciences and Engineering Research Council of Canada. We thank Pierre Bertrand for his help with the figures.
Correspondence concerning this article should be addressed to C.M.S. Plowright, School of Psychology, University of Ottawa, Ottawa, Ont., K1N 6N5. (cplowrit@uottawa.ca).

rotated by 45° when presented at a visual angle of 50° degrees) can be discriminated by bumblebees, but only if prior training with different patterns (e.g., a square and a chevron) is given (Perreault & Plowright, in press). (3) Finally, the third is another way of building on the first: after training on a pattern discrimination (S+ vs. S-), bees are given more than one test. This method has been applied successfully to show, for example, that for honeybees (Gould, 1988) and for bumblebees (Korneluk & Plowright, 1995) there is a "facultative mirror image ambiguity", at least for some floral patterns: while a previously rewarded pattern and its mirror image are not confused, in the absence of the S+ the mirror image is chosen over a new stimulus, which shows that it is accepted as a substitute for the S+. The same is true for choice of a left-right transposition of a floral pattern by bumblebees (Plowright, 1997) and honeybees (Stach & Giurfa, 2001). The strategy of manipulating testing conditions following S+ vs. S- learning was also used to address the question of recognition of rotated patterns (Plowright et al., 2001). In this paper, we combine all three strategies. Four groups of bees were trained on a pattern discrimination (S+ vs. S-), the training experience was manipulated, and the testing conditions were manipulated as well. The use of a design that manipulates training and testing conditions factorially preserves all the strengths of the three approaches delineated above, with the added advantage of being able to detect an interaction between training and testing conditions.

Prior research has pointed to a dorso-ventral asymmetry in pattern perception in honeybees (Wehner, 1972) and bumblebees (Thivierge, Plowright, & Chan, 2002) with stronger weighting of the ventral portion. Prior research has also shown that for honeybees, differential conditioning (S+ vs. S-), as opposed to absolute conditioning (no alternative to the S+), results in an increase in the visual field assigned to the visual recognition task (Giurfa et al., 1999). Here we extend the research by attempting to manipulate the relative weighting of the inferior and superior portions of the patterns within a differential conditioning task. We created two sorts of patterns (shown in Figure 1), both for training and for testing: (1) those that were identical above the midline (so identical superior portions of the S+ and the S-) and could only be distinguished by attention to the inferior portions (2) those that could only be distinguished by attention to the superior portions, the inferior portions being identical. Depending on the contents of learning during training, several possible experimental outcomes can be envisaged, three of which are described below (see Predictions).

Method

Subjects

Three colonies of bumblebees (*Bombus impatiens*) were purchased from Biobest Canada, Ltd (Leamington, Ont.). Bees were individually labeled with coloured tags glued to the thorax. They were fed with sugar solution (2:1 sugar and water by volume) and pollen *ad libitum*. The supply of sugar solution was removed one day before training and testing periods to motivate foraging behaviour.

Apparatus

A 12-arm radial arm maze was used. It was modelled on that of Lehrer, Horridge, Zhang, and Gadagkar (1995), diagrammed in Séguin and Plowright (2008) and described by Simonds and Plowright (2004) and by Plowright, Simonds, and Butler (2006). One advantage of using this maze over the Y-maze is that it increases the frequency of exposure to the S+ and S- within one visit to the maze (Perreault & Plowright, in press). Each corridor (14 X 15 X 15cm, W X L X H) opened onto a central area (22cm wide). The corridors' entrances from the central area were 6 cm wide. The vertical walls of the maze were made from opaque grey Plexiglas. The maze was connected through one corridor (the entrance corridor) by a wooden walkway covered with glass plates. Once a bee had entered the maze, the entrance corridor was blocked off, as was the corridor facing the entrance corridor, and so the bees made choices among the 10 remaining corridors during the experiment. The maze was positioned on a rotating platform so that with a 180° rotation, which was done four out of five times that a bee was allowed to enter the maze, the entrance corridor could be changed as could be the positions of the patterns relative to the entrance. Lighting was provided by daylight, two 32watt tubular incandescent lights located over the apparatus and fluorescent room lights.

Patterns

The four patterns were first created by Horridge (1996) and also used by Perreault and Plowright (in press): the cross (more specifically, the Saint-Andrew's cross, or the multiplication sign), the diamond (i.e., a square rotated by 45 °) and two chevrons (one pointing upwards and one pointing downwards, heretofore referred to, respectively, as the chevron-point-up and the chevron-point-down). They all consisted of two pairs of black orthogonal bars (4.3cm x 1.3cm)—since the bars were perpendicular, their orientations cancelled out, and so there was no overall orientation to the patterns that could serve to discriminate between them (Horridge, 1997). Patterns were printed on white paper (same dimensions as the end of the corridor) and laminated. A hole of 1.5cm diameter was cut through the center of each pattern for the end of the feeder tube.

Procedure

The experiment consisted of three consecutive phases (shaping, training and testing) described below. The sequence was repeated for new groups of 3-5 bees being tested until ten bees per group had been tested.

Shaping. The purpose of this phase was to allow the bees to explore the apparatus, to motivate them to forage inside, to approach the ends of the corridors and to allow us to select the most active foragers. A white square was positioned vertically on the wall at the end of each of the 10 corridors that were used in the maze. A hole (1.5cm in diameter) was pierced through the centre to allow the end of a feeding tube filled with sugar solution to protrude. Over three days, the colony was unstoppered so as to allow bees unrestricted access for 2hr inside the maze. The identities of the most active individuals were recorded so that they could be selected for training and testing.

Training. Bees were trained individually to discriminate between a rewarding pattern (S+), for which the feeder was filled with sugar solution, and an unrewarding pattern (S-), for which the feeder was filled with water. In a pilot study, presenting 10 patterns simultaneously seemed to create a "noisy" visual environment, and so we began by presenting only one S+ and one S- while blocking the other corridors, with the S+ and S- on opposite sides of the entrance. After each visit to the maze, the positions of the two patterns were changed in a pseudo-random order. A choice was defined as contact between the antennae or the proboscis and the feeder. When a bee had met a criterion of 12 choices of the S+ in 15 consecutive choices, we proceeded to train the bees in an environment similar to the one they would encounter during testing, i.e., patterns were available in all 10 corridors. The same criterion of 80% choices of the S+ was used for 10 consecutive choices, and a bee was tested immediately after training.

Testing. All feeders were filled with water and the training patterns were replaced with new testing patterns. Only one visit to the maze was allowed and the test concluded when the bee had made 15 pattern choices or had stopped foraging for 5 minutes.

Design

Training and testing conditions were manipulated factorially in a 2 X 2 between groups design (Figure 1). During training, the S- was the cross. The S+ was either a chevron-point-down or the chevron-point-up. In this way, the difference between the S+ and S- was either in the positions of the two lines in the inferior (Inf) or superior (Sup) portion of the pattern (these portions are framed in Figure 1). During testing, the choice was between a diamond and another pattern (again, the chevron-point-down or chevron-point-up). In this way, the difference between the two patterns was again either in the positions of the two lines in the inferior or superior portions of the pattern. The remaining lines, that did not differ between the testing patterns, were oriented in such a way that the test would not consist of repeating the S+ vs. S- discrimination that had just been succeeded, if for no other reason than to avoid a ceiling effect. The four groups will be referred to as Inf-Inf, Inf-Sup, Sup-Inf and Sup-Sup, with the labels specifying first the portions of the pattern that differed in training and then in testing. We examined the proportion of the choices of the diamond as a function of training and testing.

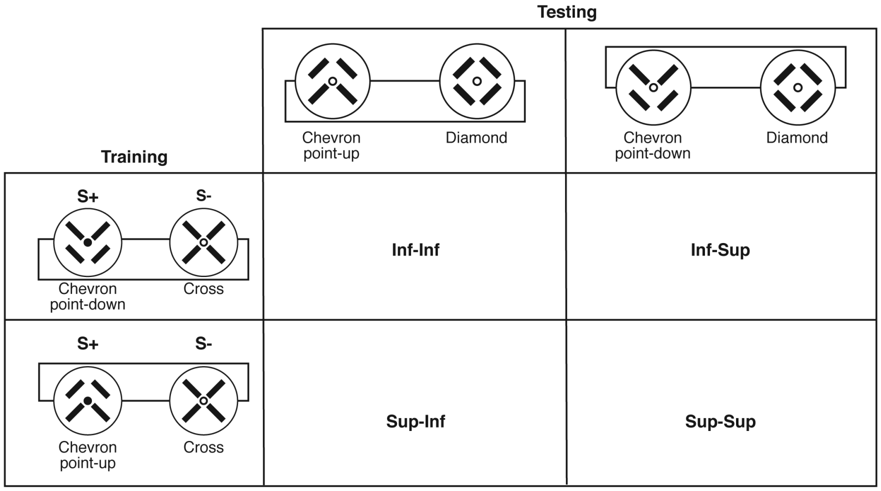

Figure 1. Training and testing stimuli used for each of four groups of bumblebees. The circle at the center of each pattern shows the position of the feeder. An open circle shows that the feeder contained only water and a full circle shows that it contained sugar solution. Either the inferior (Inf) portions or the superior portions (Sup) differed within a pair of patterns. To highlight the difference these portions are framed.

Predictions

Depending on what bees learned during training, at least three experimental outcomes were possible:

(1) The naïve notion that during training the bees would learn a rule "Approach the pattern that was rewarded during training" predicts that during testing, bees would only succeed in discriminations where a copy of the S+ was presented (Groups Inf-Sup and Sup-Inf) but would fail when two new patterns were given (Groups Inf-Inf and Sup-Sup).

(2) If our training manipulation were successful in shifting attention away from the inferior towards the superior portions of the patterns, then testing performance would depend on the match between the training and the testing conditions: the bees in groups Inf-Inf and Sup-Sup should be more successful in the test discriminations. This prediction is the opposite of the first. The prediction is strong in that the dorso-ventral symmetry documented in the literature would have to be so malleable as to be reversed by prior experience.

(3) A third possibility is that training bees to attend to the superior portion of the patterns would not shift the attention away from the inferior portion so much as extend it to encompass more of the visual patterns. This prediction differs from the effect, already documented for honeybees by Giurfa et al. (1999), that pattern encoding differs under conditions of differential conditioning vs. absolute conditioning. Here, our manipulation of training conditions occurs within a differential conditioning task. There still might be a dorso-ventral asymmetry, with the inferior portion of the pattern being weighted relatively more strongly than the superior portion, but nonetheless, the superior portion of the pattern would matter.

Training the bees to discriminate between patterns that differed in their inferior portions would only allow them to distinguish patterns that differed in their inferior portions (group Inf-Inf) but not their superior portions during testing (group Inf-Sup). Training them to discriminate between patterns that differed in their superior portions would allow the bees to make similarity judgments between the testing stimuli and the training stimuli based on both the inferior and superior portions of the stimuli. If a copy of the S+ were present at testing (the chevron-point-down), then it ought to be preferred over the diamond (group Sup-Inf). The behaviour towards the diamond, however, should be context specific. The diamond would become more attractive in the absence of a copy of the S+ (group Sup-Sup). The diamond would now become the stimulus that most resembled the S+ and, conversely, the chevron-point-down would most resemble the S-.

Statistics

Choice proportion of the diamond vs. the alternative pattern is a binary variable, and so a logistic model, which specifies a binomial error term, was fit to the data using GLIM (Generalized Linear Interactive Modelling; Francis, Green, & Payne, 1993) to determine whether the choice proportion of the diamond depended on training and testing.

To determine whether two patterns at testing could be discriminated, a replicated goodness-of-fit test with the G-statistic was used (Sokal & Rohlf, 1995) because the data set consisted of repeated choices by individual bees. Two G values were obtained: G_H and G_P. The G_H value tests for heterogeneity (i.e., individual differences). The G_P value tests for whether the pooled data (i.e., the group choice proportions) deviated from a theoretical value of chance (50:50). The G values are compared to a χ^2 value in tests of significance.

Results

Figure 2 shows the mean choice proportions for the diamond for each of the four experimental conditions. The main effect of training condition was significant ($X^2_{(1)} = 17.71$, $p < 0.0001$) while the main effect of testing condition was not ($X^2_{(1)} = 0.13$, $p = 0.72$). The presence or absence of main effects, however, are comparatively uninformative in view of the significant interaction ($X^2_{(1)} = 34.62$, $p < 0\ .0001$). The top two bars show the choices of the two groups that had been trained to discriminate between the chevron-point-down (S+) and the cross (S-). The diamond, though it had not been presented during training, was preferred during testing over the chevron-point-up (group Inf-Inf). This preference was eliminated, however, when the alternative was the chevron-point-down (group Inf-Sup). The bottom two bars show the choices of the two groups that had been trained to discriminate the chevron-point-up (S+) from the cross (S-): the preferences for the diamond “move” in the opposite direction. In marked contrast with the group Inf-Inf, the diamond was distinctly avoided compared to the chevron-point-up (group Sup-Inf). The preference increased (i.e., the avoidance disappeared) when the alternative was the chevron-point-down (group Sup-Sup).

The analysis above compared the four groups to each other. The following analysis compares the choice proportions of each group to a chance value of 50:50. Table 1 shows the results of the G-test for each of the four experimental conditions. For the two groups tested with the chevron-point-up and the diamond, the discrimination was significant. The preferences shown, however, were in opposite directions: Group Inf-Inf favoured the diamond over the chevron-point-up, whereas group Sup-Inf did the reverse. For the two groups tested with the chevron-point-down and the diamond (groups Inf-Sup and Sup-Sup), the choice proportions did not differ significantly from chance. No individual differences were detected in any of the four groups: G_H was non-significant in all cases.

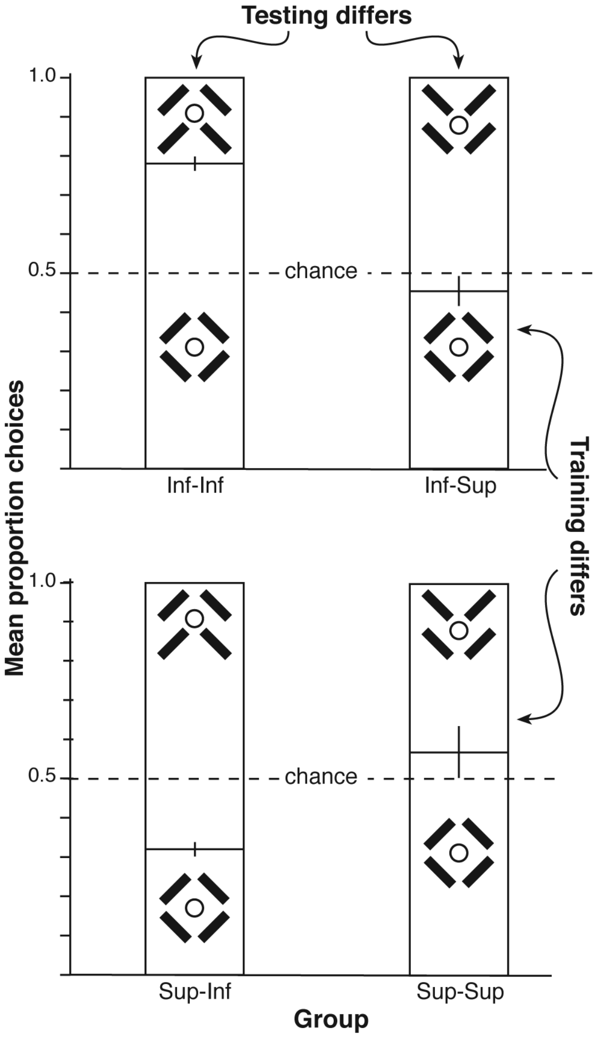

Figure 2. Choice proportions, with standard error bars, for the test stimuli for each of the four groups shown in Figure 1. Table 1 shows which proportions differed from a chance value of 0.5. The interaction between training and testing was significant.

Table 1.

Results of the repeated measures G test for the four experimental conditions. The G_P value tests for a deviation between the observed choice proportion for the diamond shown in Figure 1 and a chance value of 0.5. The G_H value tests for individual differences. In the tests of significance, the G value is compared to a χ^2 value.

Group	G_P (1 df)	*p*	G_H (9 df)	*p*
Inf-Inf	32.44	< 0.0001	5.98	0.74
Inf-Sup	0.41	0.52	8.51	0.48
Sup-Inf	18.67	< 0.0001	3.90	0.92
Sup-Sup	1.45	0.23	14.25	0.11

Discussion

For visual pattern discriminations, the effects of training and testing conditions can not be understood independently. The effect of manipulating testing conditions was to reduce a preference for a diamond given one type of training but to increase that preference given another. The same interaction can be described as a significant effect of type of training given one testing context, and an absence of such effect in another. The effects reported above were not attributable to particularities of a few individuals, since individual differences were non-significant in all the analyses, and bees from three different colonies were used. The implications of this interaction in terms of how patterns are encoded are described next with reference to the three predictions outlined above.

The first two of our predictions were disconfirmed. Specifically, a simple rule such as "approach the pattern that was rewarded during training" predicted a discrimination between the two test patterns by the group Inf-Sup because a copy of the S+ was present during the test. No discrimination was obtained. More importantly, the rule predicted a failure in discrimination by the group Inf-Inf because a copy of the S+ was absent during the test. In our experiment a strong preference for the diamond was obtained. The second prediction was the opposite of the first, and it did not fare better. If training with patterns that differed either in the superior or the inferior portions of the patterns served to shift the attentional focus of the bees, then only patterns that differed in the same areas as in training would be differentiated at the time of testing; i.e., successful discrimination would be obtained only for groups Inf-Inf and Sup-Sup. In fact, groups Inf-Inf and Sup-Inf succeeded while Inf-Sup and Sup-Sup failed.

Our data are in line with the third prediction. If bumblebees are indeed disposed to weight the inferior portion of the patterns, then training with patterns that differed only in the inferior portion would lead to a discrimination by the group that was shown patterns that differed in the inferior portion at the time of testing (Group Inf-Inf) but not by the group that was shown patterns that differed in the superior portion (Group Inf-Sup). This is exactly what happened. Training with patterns that differed in the superior portion would not shift attention so much as expand it to include not only the inferior but, to a certain extent, the superior portion as well. This would predict a preference for the chevron-point-up over the diamond by group Sup-Inf, since both inferior and superior portions are the same as the previously rewarded stimulus. This preference was obtained. It would be at the very least reduced if not eliminated or reversed by group Sup-Sup since the superior portion of the diamond corresponds to the superior portion of the S+ and the superior portion of the chevron-point-down corresponds to the superior portion of the S-. This effect too, was obtained.

The fact that the choice proportion by group Sup-Sup was not significantly greater than chance, though it was in the predicted direction, is in no way incompatible with our explanation. It merely shows that the representation of the superior portion of the patterns was still weak relative to the inferior portion. Both testing patterns would have been unattractive by virtue of the dissimilarity between the inferior portions of both patterns to either the S+ or the S-. The possibility that the training with the superior part of the patterns may have taken longer than the training with the inferior parts in no way detracts from our arguments either. When the extent of training is explicitly manipulated, it does affect pattern encoding (Stach & Giurfa, 2005). In our experiment, training length was not manipulated but if the bees were predisposed to attend to the inferior portions, then the bees may have adjusted learning time to attain a learning criterion themselves: it may well have taken them longer to locate the portions of the training patterns that afforded a key to the discrimination.

Using just the four patterns in this experiment, it would be possible to train the bees on six different S+ vs. S- combinations. If making all these comparisons becomes necessary in the future, then our results point to the importance of manipulating not only the training stimuli but also the test stimuli. With the same six combinations of test stimuli, it would have been possible to obtain 36 choice proportions to compare with each other. Making such comparisons was beyond the scope of this paper, and our conclusions are limited to (1) the hypotheses described above, and (2) the general point that in the presence of a significant interaction between training and testing conditions such as the one documented here, conclusions regarding the effect of training in one particular context, or for that matter the effect of testing context after one particular learning experience, must be carefully circumscribed.

Our results should be interpreted with two cautions, both of which have been made by Giurfa et al. (1999) in their study demonstrating the effect of absolute vs. differential conditioning on visual recognition. The first is that no claim is made as to the nature of coding of the stimuli. The issue of whether visual patterns are represented as a set of unassembled features or an image that preserves the spatial layout of those features has been explored at length elsewhere (e.g., Srinivasan, 1994; Efler & Ronacher, 2000; Horridge, 2000; Stach, Benard, & Giurfa, 2004). The second is that the superior and inferior portions of the patterns do not necessarily correspond to the dorsal and ventral portions of the insect's visual field. Given that the feeders were in the center of vertically positioned patterns, it stands to reason nonetheless that the inferior portion of the pattern was detected in a more ventral portion of the visual field than the superior portion.

In terms of ecological significance, this study provides a laboratory demonstration of relative preferences (for review of factors influencing floral choices, see Goulson, 2003). A floral pattern can not be thought of as attractive to bees in an absolute sense: its drawing power depends on prior experience, present context, and the combination of the two. By showing that bees do find the relevant cues that will allow them to differentiate sources of food from unrewarding patterns, this study also highlights the problem solving nature of learning, and so it is particularly relevant to current efforts to understand bumble bee foraging by integrating the study of cognition and behavioural ecology (e.g., Chittka & Thomson, 2001; Dukas, 2008). It does, however, raise a question that is traditionally the province of psychology: What is the effective stimulus and what are the cognitive processes that give rise to its perception and retention? While these questions belong to mainstream animal learning (Fetterman, 1996), "bee cognition" (e.g., Cheng, 2000; Gould, 1990, 2002) has not always made contact with other-animal-cognition (and more generally, comparative psychology has not always made contact with cognitive psychology (Smith, 2003)). As noted by Bitterman (1996, p. 123) not so long ago, “zoologists interested in invertebrates have not been much interested in learning” and “psychologists have not been much interested in invertebrates”. Much headway has been made in recent years. For instance, the binding problem in perception has recently been addressed for bees (Fauria, Colborn, & Collett, 2001) as have the topics of working memory (Brown & Demas, 1994), concept formation (Giurfa, Zhang, Jenett, Menzel, & Srinivasan, 2001) and timing (Boisvert & Sherry, 2006). Nonetheless, for the sake of argument, we suggest the following point for debate: that questions in bee cognition are still currently constrained by an inward looking perspective that may well have been born, understandably, from a deliberate attempt to avoid species generalizations and especially generalizations from vertebrates to invertebrates. The benefits of integrating bee cognition with other disciplines such as behavioural ecology (Dukas, 1998; Dukas & Ratcliffe, in press; Chittka & Thomson, 2001), neuroscience (Menzel, 2001) and robotics (Srinivasan & Venkatesh, 1997) are undeniable, but bee cognition is, after all, cognition, and it remains to be fully integrated with its own field.

References

Benard, J., Stach ,S., & Giurfa, M. (2006). Categorization of visual stimuli in the honeybee *Apis mellifera*. *Animal Cognition*, **9**, 257-270.

Bitterman, M. E. (1996). Comparative analysis of learning in honeybees. *Animal Learning* & *Behavior*, **24**, 123-141.

Boisvert, M. J. & Sherry, D. F. (2006). Interval timing by an invertebrate, the bumble bee *Bombus impatiens*. *Current Biology*, **16**, 1636-1640.

Brown, M. F. & Demas, G.E. (1994). Evidence for spatial working memory in honeybees (*Apis mellifera*). *Journal of Comparative Psychology*, **108**, 344-353.

Cheng, K. (2000). How honeybees find a place: Lessons from a simple mind. *Animal Learning & Behavior*, **28**, 1-15.

Chittka, L. & Thomson, J. D. (2001). *Cognitive ecology of pollination*. Cambridge: Cambridge University Press.

Church, D. L. & Plowright, C. M. S. (2006). Spatial encoding by bumblebees (*Bombus impatiens*) of a reward within an artificial flower array. *Animal Cognition***, 9**, 131-140.

Dukas, R. (1998). *Cognitive ecology*. Chicago: University of Chicago Press.

Dukas, R. (2008). Evolutionary biology of insect learning. *Annual Review of Entomology*, **53**, 145-160.

Dukas , R. & Ratcliffe, J. M. (in press). *Cognitive Ecology II*. Chicago: University of Chicago Press.

Dyer, F. C. (1998). Spatial cognition: Lessons from central-place foraging insects. In: Balda R. P, Pepperberg, I. M, Kamil, A. C. (Eds), *Animal cognition in nature: The convergence of psychology and biology in laboratory and field* (pp.119-154) Toronto: Academic Press.

Efler, D. & Ronacher, B. (2000). Evidence against a retinotopic-template matching in honeybees’ pattern recognition. *Vision Research*, **40**, 3391-3403.

Fauria, K., Colborn, M., & Collett, T. S. (2000). The binding of visual patterns in bumblebees. *Current Biology*, **10**, 935-938.

Fetterman, J. G. (1996). Dimensions of stimulus complexity. *Journal of Experimental Psychology: Animal Behavior Processes*, **22**, 3-18.

Francis B., Green M., & Payne C. (1993) *GLIM: The Statistical System for Generalized Linear Interactive Modelling.* Version 4.0. New York: Oxford University Press.

Giurfa, M., Hammer, M., Stach, S., Stollhoff, N., Müller-Deisig, N., & Mizyrycki, C. (1999). Pattern learning by honeybees: Conditioning procedure and recognition strategy. *Animal Behaviour*, **57**, 315-324.

Giurfa, M., Zhang, S., Jenett, A., Menzel, R., & Srinivasan, M. V. (2001). The concept of sameness and difference in an insect. *Nature*, **410**, 930-933.

Gould, J. L. (1988). A mirror-image ‘ambiguity’ in honey bee pattern matching. *Animal Behaviour*, **36**, 487-492.

Gould, J. L. (1990). Honey bee cognition. *Cognition,* **37**, 83-103.

Gould, J. L. (2002). Can honeybees create cognitive maps? In M. Bekoff, C. Allen & G. M. Burghardt (Ed.), *The cognitive animal: Empirical and theoretical perspectives on animal cognition* (pp. 41-45). Cambridge, Massachusetts: MIT Press.

Goulson, D. (2003). *Bumblebees: Behaviour and Ecology*. Oxford: Oxford University Press.

Horridge, G. A. (1996). Vision of the honeybee *Apis mellifera* for patterns with two pairs of equal orthogonal bars. *Journal of Insect Physiology***,** **42**, 131-138.

Horridge, G. A. (1997). Spatial and non-spatial coding of patterns by the honeybee. In M. V. Srinivasan, & S. Venkatesh (Eds.), *From living eyes to seeing machines* (pp. 52-79). Oxford: Oxford University Press.

Horridge, A. (2000). Seven experiments on pattern vision of the honeybee, with a model. *Vision Research,* **40**, 2589-2603.

Horridge, G. A. (2005). What the honeybee sees: A review of the recognition system of *Apis mellifera. Physiological Entomology,* **30**, 2-13.

Horridge, A. (2007). The preference of the honeybee (*Apis mellifera*) for different visual cues during the learning process. *Journal of Insect Physiology,* **53**, 877-889.

Korneluk, Y. G. & Plowright, C. M. S. (1995). Mirror image pattern matching by bumble bees. *Behaviour,* **132,** 87-93.

Lehrer, M., Horridge, G. A., Zhang, S. W., & Gadagkar, R. (1995). Shape vision in bees: Innatpreference for flower-like patterns. *Philosophical Transactions of the Royal Society of London B,* **347**, 123-137.

Menzel, R. (2001). Searching for the memory trace in a mini-brain, the honeybee. *Learning & Memory,* **8**, 53-62.

Perreault, M .J. & Plowright, C. M. S. (In press). Facilitation of learning of a simultaneous discrimination between rotated patterns by bumblebees. *Learning & Motivation (2008), doi:10.1016/j.lmot.2008.10.001*

Plowright, C. M. S. (1997). Function and mechanism of mirror image ambiguity in bumble bees. *Animal Behaviour,* **53**, 1295-1303.

Plowright, C. M. S., Landry, F., Church, D., Heyding, J., Dupuis-Roy, N., Thivierge, J. P., & Simonds, V. (2001). A change in orientation: Recognition of rotated patterns by bumble bees. *Journal of Insect Behavior,* **14**, 113-127.

Plowright,C. M. S., Simonds, V. M., & Butler, M. A. (2006) How bumblebees first find flowers: Habituation of visual pattern preferences, spontaneous recovery and dishabituation. *Learning & Motivation*, **37**, 66-78.

Séguin, F. R. & Plowright, C. M. S. (2008). Assessment of pattern preferences by flower-naïve bumblebees. *Apidologie,* **39**, 215-224.

Shettleworth, S. J. (1998). *Cognition, evolution and behaviour.* New York: Oxford University Press

Simonds V. M. & Plowright C. M. S. (2004) How do bumblebees first find flowers? Unlearned approach responses and habituation. *Animal Behaviour,* **67**, 379-386.

Smith, J.D. (2003). Why cognitive psychologists should know comparative psychology; why comparative psychologists should know cognitive psychology. *International Journal of Comparative Psychology*, **16**, 44-63.

Sokal, R. R. & Rohlf F, J. (1995) *Biometry*, 3rd edition. San Francisco: W. H. Freeman.

Srinivasan, M. V. (1994). Pattern recognition in the honeybee: Recent progress. *Journal of Insect Physiology*, **40**, 183-194.

Srinivasan, M. V. & Venkatesh, S. (Eds.) (1997). *From living eyes to seeing machines*. Oxford: Oxford University Press.

Stach, S., Benard, J., & Giurfa, M. (2004). Local-feature assembling in visual pattern recognition and generalization in honeybees. *Nature***, 429**, 758-761.

Stach, S. & Giurfa, M. (2001). How honeybees generalize visual patterns to their mirror image and left-right transformation. *Animal Behaviour*, **62**, 981-991.

Stach, S. & Giurfa, M. (2005). The influence of training length on generalization of visual feature assemblies in honeybees. *Behavioural Brain Research,* **161**, 8-17.

Thivierge, J. P., Plowright, C. M. S., & Chan, T. (2002). Recognition of incomplete patterns by bumble bees. *Behavioural Processes*, **59**, 185-191.

Wehner, R. (1972). Dorsoventral asymmetry in the visual field of the bee, *Apis mellifica*. *Journal of Comparative Physiology,* **77**, 256-277.