General Discussion

This thesis aimed to examine the categorization capacities of visual patterns in honeybees. We attempted in this way to better characterize visual cognitive processes in the insect brain. This is an important objective in comparative cognitive studies as, for instance, the view that only some vertebrate species are capable of relational discrimination, contextual learning, expectations and abstraction, among others, is currently challenged by many results from research on insects (see Menzel & Giurfa, 2001; Giurfa, 2003a for reviews). First, I asked how bees treat certain transformations of patterns such as a mirror image and a left- right transformation of visual stimuli. In particular, I was interested by the flexible use of similar visual information when the memorized information was absent. The results showed that bees can generalize the excitatory strength of a trained pattern to the mirror-image and the left-right transformations, and also revealed the possibility that bees can combine several stimulus elements in a specific spatial configuration. This possibility was then examined, thus showing a new alternative in honeybee pattern categorization. Despite the fact that visual feature binding was repeatedly denied in the case of insects (e. g. Horridge, 1996; 1997a; 2000a; 2003; 2003a) I show that such binding is not only possible in bees but is even at the origin of configural representations that can be used for further stimulus categorization. Finally, I studied the influence of different levels of experience in the building of configural visual stimulus representations. Such a building is not a prerogative of a specific training method as that underlying the principle of learning sets (Harlow, 1949). It occurs even in cases in which bees are conventionally trained with a single pair of patterns, providing that their cumulative experience with the patterns is long enough.

Generalization to pattern transformations

The first chapter of this thesis was concerned by how certain pattern transformations such as mirror-images and left-right transformations of a given pattern are perceived and treated by honeybees, when the corresponding original pattern previously trained was not available. In natural conditions, generalization of the search image of a flower to some of its transformations could be adaptive. The shape of flowers can underlie considerable changes due to missing or occluded flower parts, differences in distance or angle of approach or other distortions. The capacity to generalize the excitatory strength of a given flower shape to some of its visual transformations constitutes a flexible strategy that allows to solve this kind of problems.

These transformations are commonly used in generalization experiments because some animals show an ambiguity for the mirror image and the left–right transformation of an asymmetric pattern (Sutherland, 1969; Warren, 1969; Hamilton et al., 1973; Todrin & Blough, 1983; Hollard & Delius, 1982) (Chapter I). In other words, when confronted to these transformations, some animals respond to them as if they were the original trained or searched stimulus, thus showing a capacity for flexible stimulus use. The results of my experiments show that bees trained to a single pair of patterns as well as to a random sequence of six different pairs of patterns (Chapter I, Fig. 2a, b) preferred the mirror-image and the left-right transformation of the rewarded stimulus or group of stimuli to a chequerboard pattern (a neutral stimulus) (Chapter I, Fig. 2c) when the learned stimulus was absent (Chapter I, Figs. 4 and 6). Moreover, after both kinds of training, they preferred the left-right transformation to the mirror-image (Chapter I, Figs. 4 and 6) whenever these were presented together. In the case of vertebrates, this visual ambiguity for certain image transformations was related to the symmetric structure of nervous systems (Corballis & Beale, 1970). Due to the symmetric structure of the nervous system information has to be

transferred from one half to the other. Corballis and Beale (1970) assumed that this transfer is so complete that animals have difficulty in discriminating mirror images from the original. There is experimental evidence from testing the effects of commissurotomy on left-right mirror-image discrimination which suggests that the interhemispheric commissural connections between the two brain hemispheres, by allowing lateralised signals to intermix, contribute to such difficulty (Beale et al., 1972; Achim and Corballis, 1977). On the other hand, this kind of ambiguity has been repeatedly associated with higher cognitive processes such as mental rotation, the capacity of mentally changing the orientation of an image in order to reassess it from a new imaginary perspective (Shepard & Metzler 1971; Cooper & Shephard, 1973; Cooper 1975; Cooper & Podgorny, 1976; Hollard & Delius, 1982; see Chapter I). In the case of the honeybee, the explanation provided for such an ambiguity does not invoke mental rotation processes. The processes involved in left-right transformation and mirror image generalization seem to be based on "lower" processes such as the integration of pattern features into a simplified configuration and comparison of the resulting representation with the currently perceived image. The results of experiments 2 and 3 of the first chapter led to the idea that the training stimuli could be learned in terms of a specific spatial configuration of the four orientations presented in the training stimuli. This assumption is supported by the results of experiment 3, in which bees generalized orientation information to reduced stimulus versions (Chapter I, Fig. 2d) and in appropriate tests preferred the one having more coincidence with the configuration of the rewarded group of training stimuli, i.e. they preferred the left-right transformation over the mirror-image (Chapter I, Figs. 7 and 8).

These results allowed proposing a new hypothesis on visual stimulus representation in the case of insects. In fact, although integrating features into a global representation may

be a low process, the flexible use of the resulting representation to categorize and thus respond appropriately to novel patterns is not.

The configural pattern representation hypothesis

This option was further investigated and demonstrated in Chapter II. Here, bees were trained with the same randomised sequence of six pairs of patterns (Chapter II, Fig. 1a) as used in the experiments described in Chapter I, in order to suppress the use of a retinotopically fixed template and to promote feature extraction. The basic assumption was that this kind of training was necessary to implement an abstract pattern representation such as the configural one. Although this assumption was essentially correct, we showed later that even simpler forms of training can lead to the same representation provided that the amount of the experience with the training stimuli is enough (see Chapter III). In order to test, whether bees extracted the configuration of the four orientations presented in the training stimuli and used to respond (categorize) to novel stimuli, they were presented with reduced versions of the stimuli, similar to those used in Chapter I (Chapter I, Experiment 3), one corresponding to the rewarded configuration and the other corresponding to the rewarded configuration with one of the four bars rotated by 90°, thus resulting in four possible configurations, which were each presented in a different test (Chapter II, Fig. 1b). All the test stimuli were new to the bee. Only one belonged always to the category defined by the trained configuration (positive configuration), thus preserving the principle of a transfer test, necessary to determine whether categorization occurs or not. In all cases, the bees preferred the complete positive configuration over the one with one rotated bar (Chapter II, Fig. 2b). This result is consistent with the result of experiment 3 in Chapter I, in which the bees preferred the left-right transformation to the mirror-image when they were presented against each other (Chapter I, Figs. 7 and 8). In the left-right-

transformation all four orientations correspond to the rewarded training configuration, with the left and the right sides interchanged. The mirror-image contains two orientations corresponding to the negative training configuration (see Chapter I, Fig. 2d). Each of the configurations with one bar rotated has one bar in common with the negative configuration (see Chapter II, Fig. 1b). An interesting question is whether bees can or not rank the stimuli as members of a given category according to the number of corresponding orientations with respect to the positive or the negative configuration. In other words, whether categorization of a positive configuration (four correct orientations in the appropriate spatial relationship) is flexible enough to make the bees prefer a novel pattern with three correct orientations to one with two or only one correct orientation. Although the results of experiment 3 of Chapter I and experiment 1 of Chapter II could provide a first idea concerning this generalization beyond the limits of a category, they do not allow direct comparison, because the mirror-image transformation additionally includes a switch of the right and left side with respect to the original positive configuration.

In any case, Chapter II showed, for the first time, that bees can implement a form of visual stimulus representation, different from the two classical alternatives known up to now, 1) template building and matching and 2) single-feature extraction and matching. In this new hypothesis, bees combine features to generate a global simplified pattern representation. Obviously, as in the previous alternatives a comparison between the perceived and the memorized image has to occur (matching) but the possibilities arising for responding to novel, similar stimuli are much higher than in retinotopically template building and matching. In the same way, the combinatorial possibility available in a configural representation increases the accuracy of the decision of whether a given stimulus belongs or not to a certain category. In other words, if bees used a single feature to choose between patterns in our experiments (i.e. one of four orientations), the

probability of choosing negative, non-rewarded patterns would be much higher than if choosing on the basis of the correct complete configuration.

In the introduction, three current hypothesis on categorization have been introduced. In some way, all three possibilities can explain the bees' performance. The feature theory claims that membership of a category is determined by whether or not an individual instance possesses some necessary set of defining features (Smith & Medin, 1981). In our case, the defining set of features are the four orientations at a specific position. If the complete set of features (the complete positive configuration) is presented against an incomplete set of features (the positive configuration with one rotated bar), the bees prefer the complete version of the alternatives (Chapter II, Experiment 1, Chapter III, Experiment 3). This again raises the question of whether bees rank stimuli according to the number of features contained in a presented stimulus. Although the results of experiment 3 of Chapter I and experiment 1 of Chapter II could provide a first idea concerning this kind of ranking, they do not allow direct comparison, because the mirror-image transformation additionally includes a switch of the right and left side with respect to the original positive configuration. Also experiment 4 in Chapter III could give a hint on this question. In this experiment, the configuration with one bar corresponding to the positive and three bar corresponding to the negative training configuration, bees clearly prefer the one sharing one feature with the positive configuration. A set of features indicating the membership to a category could therefore indeed account for explanations of our results.

On the other hand, the exemplar based theory (Medin & Schaffer, 1978; Pearce, 1988; Astley & Wasserman, 1992) could also explain our results. If one assumes that bees could learn all stimuli during training and afterwards generalize to novel instances according to the similarity with the known stimuli, performances such as those found in our work could be found; however, an economy principle could be invoked against this

theory. In the experiments in which six pairs of patterns were randomly presented during training, bees should memorize not only six positive stimuli, but also six negative stimuli. Thus, twelve stimuli should be learned and preserved separately and simultaneously in memory. Clearly, solutions like that proposed by the feature theory seem to be more parsimonious than that proposed by the exemplar based theory. If the bees developed a single category representation including the four orientations combined in a specific spatial configuration, their categorization performance could also be interpreted in favour of the prototype (Posner & Keele, 1968). The prototype theory claims that each category is represented in terms of a prototype, i.e. an average or central tendency. This kind of representation would then be applied to unknown stimuli and evaluated according to their similarity with the prototype. As a consequence, stimuli with a closer similarity to a prototype would be categorized easier then stimuli with lower similarity to the prototype. This statement leads back to the question of whether bees are able to rank stimuli, this time not according to the number of common features but according to similarity with a prototype. From the experimental point of view, these two possibilities are difficult to separate because a prototype of a category is likely to share the same features as the different members of the category.

The effect of training and cumulative experience

In the next chapter (Chapter III), I examined, whether or not the building of a configural stimulus representation and its use for categorization of novel stimuli is a direct consequence of the training procedure. The training with a randomised sequence of different pattern pairs is adapted from the general principle of the learning set procedure (Harlow, 1949) in which animals are subjected to a random variation of parameters except for that defined by the experimenter, which defines a specific and constant outcome that

the animal has to detect and learn. Under these circumstances, the training practically forces the bees to use the common orientation configurations, because all other parameters are varied and cannot be used to solve the task. The strategy adopted by the bees is therefore imposed by the experimenter. The recurrent question under these conditions is whether the strategies exhibited by animals to solve a problem are "natural" or not. In other words, could bees implement such a flexible pattern representation if trained in a simpler way? Training the bees to a constant pair of patterns does not impose explicitly the extraction of a specific feature as any available cue can be used to discriminate between patterns. In Chapter III, I asked whether or not configural categorization based on the extraction of four different edge orientations arranged in a specific spatial relationship also occurs if honeybees are trained with only a single pair of stimuli and, if yes, whether or not different levels of experience determine changes in the discrimination strategies employed by the insects.

The results show that even a simpler training (training to a single, constant pair of patterns) promotes the extraction of the configuration of orientations such that categorization of novel stimuli is thereafter possible if the cumulative experience with the patterns is long enough. The building of a configural visual stimulus representation therefore seems not to be a latent capability, which only occurs if bees are forced to apply it, but a "natural" strategy that results from cumulative experience with one and the same flower morph and that leads to efficient foraging. In this sense, the fact that bees are flower constant (Grant, 1951; Waser, 1986; Chittka et al., 1999) and therefore search and exploit repeatedly the same species as long as it is profitable in terms of nectar and pollen reward will certainly contribute to the building of a simplified representation of the flower exploited. As shown by our results, cumulative experience with a given stimulus, as underlying flower constancy, is critical for the building of such representation. Only after

the long training procedure applied in Chapter III (Experiments 1 and 2, Chapter III) bees responded to the reduced version of the patterns. This fact indicates a change in strategy towards a higher degree of generalization with increasing experience. A similar effect has been found in another visual discrimination problem to which free-flying honeybees were trained (Giurfa et al., 2003). In this case bees were trained with rewarded coloured discs following the scheme A+, BC+ (A, B, and C being different coloured discs and + meaning reinforcement) and then tested under extinction conditions with AB vs. BC. This particular test was conceived as it allows different predictions depending on how bees establish the associative links between the colours and the reinforcement. If the bees simply associate each colour separately with the reward they should prefer AB to BC (for calculation of associative strengths and theoretical predictions see Giurfa et al., 2003). But if they treat the compound of two colours as being an entity different from the simple sum of its representations, they should prefer BC to AC. The latter option refers to the so-called configural processing in learning theories (Pearce, 1987). Here it is worth underlining that the term "*configural*" means something different when compared to the topographical sense that it received along this thesis. Here it is not a specific configuration, which is meant, i.e. an assembly of features in a given spatial relationship, but a specific way of processing and linking stimuli between them and with the reinforcement. In any case, the work of Giurfa et al. (2003) is consistent with our work in showing that cumulative experience with the same problem leads to a change in stimulus representation, or, in this case, in the processing of such stimuli. With only few training trails, bees preferred AB to BC, thus prioritising elemental processing, but with longer training they preferred BC to AC thus prioritising configural (*sensu* Pearce) processing. The effect of cumulative experience on stimulus representation can also been found in humans. In a study on categorization in humans (Gauthier et al., 1998) individuals were trained to categorize so-

called greebles. Greebles are computer generated figures which can be varied along specific features in a controlled manner. The categorization task included three levels: recognition of individual greebles, family membership, and gender membership. It turned out, that greeble "novices" (subjects receiving a relatively short initial training) relied more on prominent, single features for categorization, whereas "experts" (subjects that received an extensive training) processed information configurally. The authors define the term 'configural processing' as the "ability to take into account the precise relations between different parts of objects as well as the parts themselves" (Gauthier et al., 1998), a definition which corresponds to our understanding of the term. Furthermore, experts showed a higher degree of generalization to unknown greebles than novices. This study shows that representational changes with cumulative experience appear in humans. In humans this phenomenon is related to face recognition which constitutes a special case of 'expertise' in humans (e. g. Diamond & Carey, 1986; Farah, 1992) and this may be the reason why it is difficult to find studies of this topic in species other than humans. However, representational changes with increasing experience constitute a possibility to optimise information processing and could be a common strategy.

Stimulus control and properties

In our experiments, we used four different orientations to define different pattern layouts. The advantage of using orientation cues is that they can be easily defined and controlled by the experimenter. In fact, the positive and negative patterns presented always the same elements, the only difference being the spatial distribution of these elements between the four pattern quadrants. This excluded from the beginning the use of alternative low-level cues for discrimination. Bees can normally employ visual cues such as disruption (Hertz, 1933; Horridge, 1997), bilateral symmetry (Giurfa et al., 1996) and angular

subtense (Horridge, 1996a) among others. None of these cues could help the bees to distinguish between rewarded and non-rewarded patterns as in all cases the patterns included the same visual information (i.e. the same disruption, asymmetry along a vertical axis, the same angular subtense) with just differing spatial distribution.

By using cues belonging to the same modality (edges differently oriented) we excluded problems related to different stimulus saliencies that may lead to overshadowing and thus preclude configural stimulus representations. It has to be mentioned, however, that recent findings on how orientations are perceived by honeybees are contradictory with our results and have to be discussed. Srinivasan et al. (1994) developed a functional model for the detection of global edge orientation to account for different experiments on orientation discrimination in bees. With this model it is possible to determine the global orientation of a pattern unambiguously. The model relies on the existence of three basic orientation detectors with overlapping receptive fields in the bee brain, each of them having a preferred orientation (the orientation to which response is maximal) differing by 60° (Fig. 1a). Neuronal correlates for these kinds of orientation detectors have been found some years later by Yang & Maddess (1997) in the visual neuropiles of the bee brain. The orientation detectors encode the global orientation of a pattern by means of their neural activity; i.e. a pattern that contains more than one orientation would evoke a response in which the neural activity elicited by the orientations is summed up.

As the critical information provided by our patterns was based on local orientation differences, it is worth analysing whether the global orientation detectors proposed and found for the honeybee account for our results. This analysis is important because the argument that bees perceive and bind isolated features into a global, configural representation would be weaken if it turns out that the global orientation of our two pattern categories (rewarded and non-rewarded) simply differed in their global orientation. In the

latter case, it would be more parsimonious to assume that bees simply evaluate the global orientation of patterns without any kind of configural stimulus representation. We will see in the following paragraphs that the model of global orientation analysis postulated for the honeybee cannot account for the discrimination found in our experiments.

The tuning curve of each of the three orientation detectors is described by the function:

(1) $0.5(1 + \cos 2\theta)$

where θ is the orientation of the pattern relative to the channels preferred orientation, assuming that each channel possesses an orientation tuning curve in the form of a raised cosine with a half width of 90° (Srinivasan et al., 1994) . The value of the angular half width of 90° was determined by the fact, that bees seem to be unable to discriminate between crosses having their two bars at right angles (e. g. ✖ vs. ✚) the reason being that the angular separation between the two stripes of the cross (90°) is equal to the half width of the channel's orientation tuning curve (90°). The sum of the contributions to the response from the two bars of such a cross is:

(2) $0.5[1 + \cos 2\theta] + 0.5[1 + \cos 2(\theta + 90°)] = 1.0$

which is a constant that is independent from θ (see Srinivasan et al. 1994 for review).

Applying this function to our simplified versions of the A and B patterns (which included four different orientations) used in the present experiments results in:

(3) $0.5[1 + \cos 2\theta] + 0.5[1 + \cos 2(\theta + 45°)] + 0.5[1 + \cos 2(\theta + 90°)] + 0.5[1 + \cos 2(\theta + 135°)] = 2.0$

which is also constant and independent from θ. This fact is illustrated in Fig. 1b. Because the simplified A as well as the simplified B pattern contain the same four orientations, two of them resulting in a right angle (0° and 90°, 45° and 135°) (Fig. 1c), the sum of contributions to the response from the four bars is 2.0 for both patterns. Therefore, after this model, pattern A should not be discriminated from pattern B by the bees as they have

the same global orientation (Fig. 1c). The same applies to the simplified versions of the mirror-image and the left-right transformation (Fig. 1c, transformations of pattern A are given as example), which should not be discriminated neither one from the other nor from the original configuration. However, the present work provides abundant evidence that bees succeed these discriminations (e. g. Experiment 3, Chapter I; Experiments 2 and 3, Chapter II; Experiment 1, Chapter III) and that, therefore, they do not base their discrimination on global orientation.
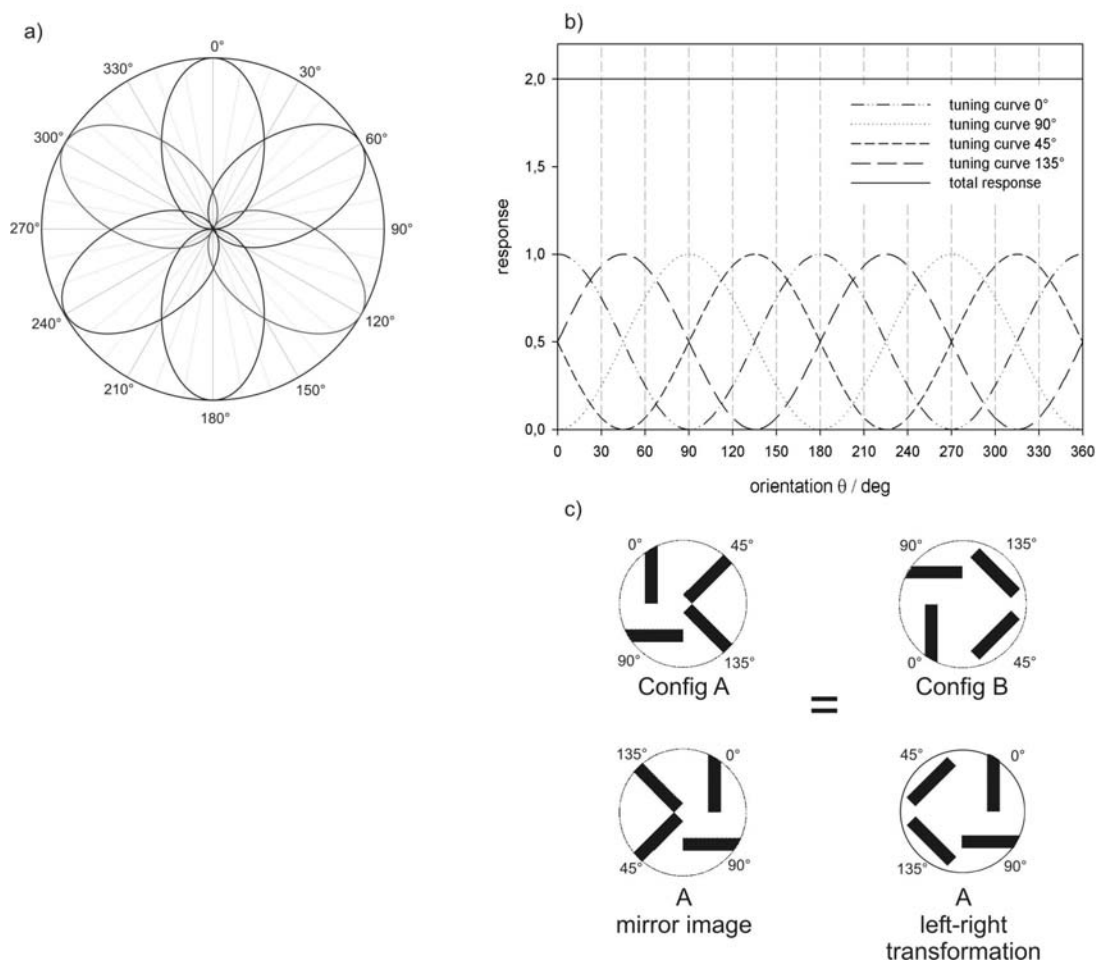

Figure 1. a) Illustration of the three hypothetical orientation detectors in the bees' visual system as proposed by Srinivasan et al. (1994). b) Modulation of the response of a hypothetical orientation detector with an angular half-width of 90°, as it views each of the configuration transformation shown in c). c) Four of the transformations used in this study, which would elicit the same constant response in a hypothetical orientation sensitive channel. Transformations of the A pattern are given as example.

Also for the orientation configurations used in Chapter II and III the response curves were
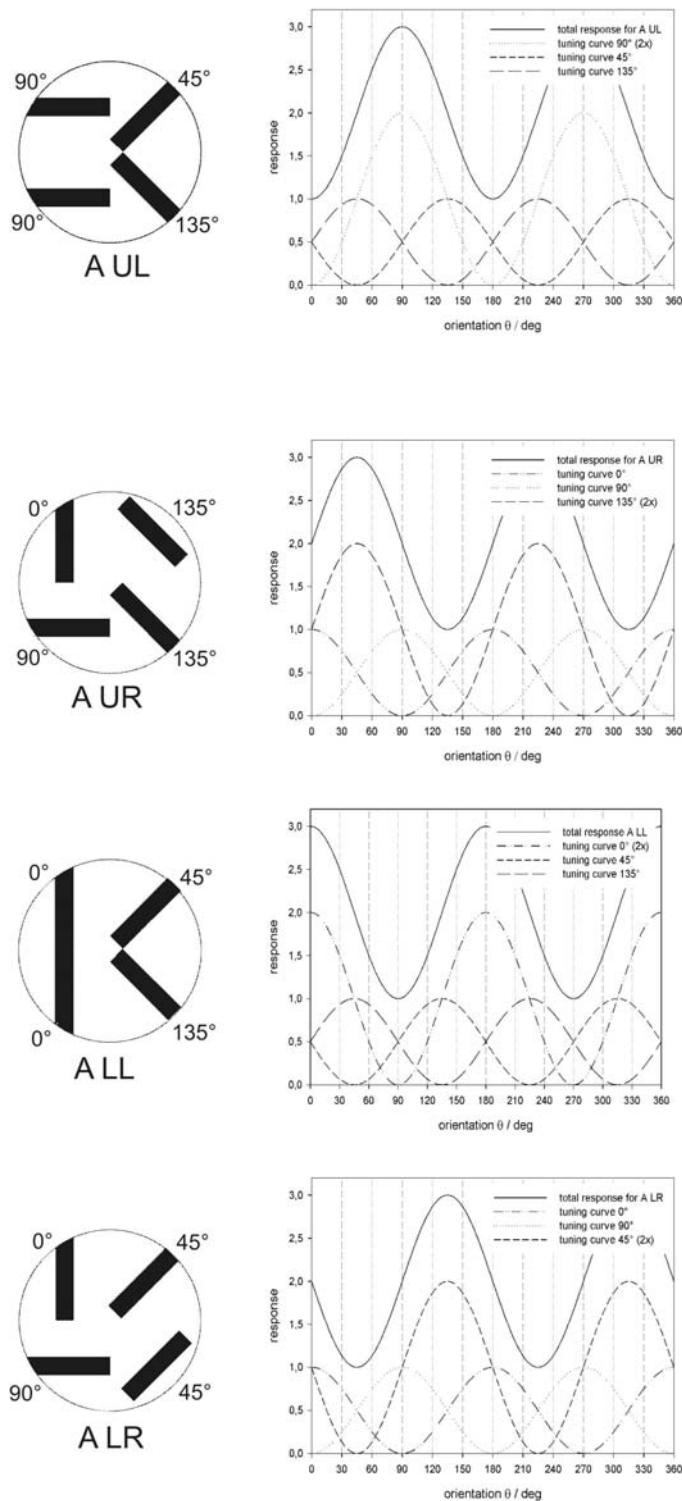
calculated (Fig. 2).

Figure 2. Modulation of the response of a hypothetical orientation detector with an angular half-width of 90°, as it views each of the orientation configuration with one rotated bar (pattern A modifications are given as example).

The response curves for the four configurations with one rotated bar are not constant, because there is only one pair of orthogonally arranged bars and one of the orientations appears twice. These patterns should therefore easily be discriminated from the complete configuration of orientations, which is actually the case (Chapter II, Experiment 1, Chapter III, Experiments 3 and 4) but also from each other. However, this model can explain neither that bees discriminate Configuration A from Configuration B nor the mirror-image and the left-right transformation from the original rewarded configuration or from each other. All in all, it can be safely concluded that although orientation differences were at the basis of pattern differences, global orientation could not be the cue used by the bees for discriminating between positive and negative patterns throughout our experiments.

One difference between our stimuli and those used by Srinivasan et al. (1994) for postulating their model on orientation analysis in the case of the honeybees is the fact that their stimuli contained exclusively orientations spanning over the whole pattern. In our study, stimuli provide different orientations associated with certain stimulus quadrants and therefore including a spatial component. In other words, local (and not global) orientation cues are critical for discrimination. The fact, that bees associate orientations with particular retinal locations has been shown in several studies (e. g. Horridge 2000, 2003). Orientation detectors with smaller visual fields are required for the implementation of an orientation configuration like the one suggested by our experiments. Such detectors have been found in the medulla of the locust *Locusta migratoria* (Osorio, 1987; James & Osorio, 1996). Two main classes of neurons identified there form numerous overlapping retinotopic arrays with receptive fields from 2 to 20°. The response of these cells allows to characterize them as edge detectors. It is thus conceivable not only that they respond to specific orientations but also that their simultaneous activation provides the basis for pattern representation in terms of a specific set of orientations.

However, the fact that bees integrate local orientation cues into a global pattern representation that preserves the spatial relationship between cues is a new finding and provides a new view in honeybee pattern recognition.

The importance of quantifying acquisition performances

Except from the experiments included in Chapter I, we obtained and showed acquisition curves for all training procedures employed in this work. The acquisition of a stimulus is an important indicator for successful learning and constitutes a critical piece of information in categorization and generalization experiments. Obviously, only animals with comparable rates of acquisition could be compared when confronted to novel stimuli. This fact underlines the importance of carefully controlling and quantifying acquisition performances in experiments involving learning processes.

Curiously, of the importance of quantifying learning success is not realized in experiments on visual pattern learning by honeybees. Although it is common use in experiments on olfactory learning by bees (probably because of the higher impact that experimental psychology methods have had on it; see Bitterman et al., 1983), biologist working on bee visual pattern learning have not yet understood that in all experiments involving visual discriminations, the experience of the animals prior to the discrimination has to be known and controlled. Among the numerous publications in this domain only few depicted acquisition performances (Giurfa et al., 2001; Chen et al., 2003; Fauria et al., 2002). In the case of Chen et al. (2003), acquisition curves are even not shown for all the training stimuli and in some cases were even obtained *a posteriori* (i.e. after the discrimination tests, using a new group of bees to this end). Although this point may appear simply technical, it is in fact critical. In this sense, it is important to point out, that this study is actually the first one in which acquisition performances were carefully controlled in the context of visual pattern

discrimination learning in bees. Especially Chapter III shows the importance of a carefully controlling the training procedure in this subject area because the results clearly show that the strategy changes with different levels of experience. This fact is new for honeybees and future studies should take it into account. In many studies, one can read "bees were trained during 2 – 3 hours" (e.g. Campan & Lehrer, 2002; Srinivasan et al., 1994) or "bees require 20 or so visits to build up a discrimination" (Horridge, 1996 - 2003) and there is no individual control over the exact number of visits of each bee. Because there are considerable changes in stimulus representation during training, this kind of procedure risks a substantial misinterpretation of the results.

Perspectives

Altogether, this thesis reveals a new possibility of visual stimulus representation in the bee brain that allows for flexible categorization of novel stimuli. However, this new possibility raises several questions, which should be answered in future projects. Some of them are listed below:

1) Flowers are complex combinations of stimulus elements belonging to different perceptual modalities. We showed that bees could combine several edge orientations, i.e. stimulus elements belonging to the same modality. But are they also able to use configurations including different modalities? To which extent can the temporal component (and thus the perceived sequence of stimuli) be implicated in the approach flight of a bee towards a flower be included in such a representation?

2) Which algorithm is used by bees to link visual features into a configural representation? This question refers to theoretical models of compound processing by animals. Recent studies have shown that bees are capable of non-elemental forms of compound processing consistent with the unique-cue theory (Deisig et al., 2001; 2002;

2003). Can this form of compound processing and learning explain the building of a global pattern representation?

3) If bees can use the strategy of feature binding, they could be in principle capable of distinguishing less abstract stimulus classes on the basis of a common stimulus layout. Feature binding into a global representation could be the basis for a classification of visual stimuli into generic categories such as "radial flowers", "closed flowers", "plant stems", as long as the members of these categories share a common feature layout. Can bees perform such stimulus classifications?

4) If bees are able to categorize novel stimuli according to their resemblance with members of a learned category, are they able to form concepts of a category? According to Lea (Lea, 1984) the term concept should be used only if the members of a category are associated with each other and not only with a response or reinforcement. He proposed that such inter-stimulus associations can be demonstrated by retraining animals with reversed reinforcement conditions (reversal learning). Such an attempt has already been effected with honeybees (Deisig, 1998) and showed that bees can build a concept of bilateral symmetry. However, this work examined the parameter symmetry and did not include stimuli that combine several elements which have to be integrated in a global stimulus representation. Can bees form concepts of stimulus configurations?

Questions like the last two were unthinkable ten years ago, when researchers interested in animal cognition focussed their attention exclusively on vertebrate models. In the last years, however, some invertebrates, and particularly the honeybee *Apis mellifera*, has emerged as a powerful model to study intermediate levels of cognitive complexity (Menzel & Giurfa, 2001; Giurfa, 2003; 2003a). Their capacity of complex learning and stimulus processing not only in the olfactory but also in the visual domain and the relative accessibility of their nervous system open a large field for further investigation.

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