

## Introduction

Most animals live in an extremely rich sensory environment in which stimuli hardly ever occur twice in exactly the same way. A crucial function of perceptual systems is therefore to record events related with relevant consequences for the animal and to signal their reappearance. This requires learning, memorisation and evaluation of perceptual input. It also requires the capacity of coping with possible distortions of the original stimuli, due to noise, extrinsic or intrinsic environmental interferences, positional or developmental changes, etc. Two strategies, which allow for flexible responding when the animal is confronted with these possible interferences, are stimulus generalization and categorization (Thorndike, 1913; Spence, 1937; Estes 1994). These two strategies allow responding in an adaptive way to novel stimuli on the basis of similarity criteria. Although, generalization and categorization are different processes, they are often deeply intermingled and a clear separation is difficult (Estes, 1994; Zentall et al., 2002). Therefore, it is necessary to provide some theoretical background information.

Generalization from past to present experience involves a measure of the similarity of present perceptual input to what has been experienced before. The evaluation of similarity is performed along a given dimension such that stimuli that lie close to each other along a perceptual scale are treated as being equivalent (Spence, 1937; Shephard, 1958). Animals processing stimuli in this way can therefore respond in an adequate manner to similar stimuli. Importantly, generalization processes imply gradual responding along a perceptual scale but not grouping of stimuli into specific classes.

Categorization, on the other hand, refers to the classification of perceptual input into defined functional groups. In this sense, it differs from the gradual decrease of responding along a perceptual scale underlying generalization. The classification into functional groups is not only a mere grouping into collections of objects, but implies

furthermore “that knowledge of the category to which an object belongs tells us something about its properties” (Estes 1994). The knowledge about a category should enable to decide whether an object belongs to a category or not. In other words, belonging to a category is defined on the basis of stricter limits than those defining generalization-based responses.

At this point, one could argue, that categorization is nothing more than generalization, because a stimulus can be assigned to a category simply depending on its similarity with a known stimulus representation. However, categorization includes a discriminative task, which demands not only the existence of a single but of at least two category representations. Keller and Schönfeld (1950) defined categorization as generalization within and discrimination between categories (Keller & Schönfeld 1950). Thus, generalization underlies categorization but the reciprocal is certainly not valid.

As this work will be concerned by categorization processes, it is worth mentioning the three main theories that have been proposed from categorization experiments in humans, to explain how stimuli are categorized.

I. The feature theory

This theory predicts that membership of a category is determined by whether or not an individual instance possesses some necessary set of defining features (Smith & Medin, 1981).

II. The exemplar theory

According to this theory the categorization of objects depends on remembering each instance or exemplar and the category to which it belongs (Medin & Schaffer, 1978).

III. The prototype theory

The prototype of a category is supposed to be a summary representation that corresponds to the average – or central tendency – of all the exemplars that have been experienced (Posner & Keele, 1968).

For each of these theories experimental evidence has been found (e. g. D'Amato & Van Sant, 1988; Vaughan & Greene, 1984; Posner & Keele, 1968). However, it is difficult to clearly separate them, because their predictions concerning the outcome of experiments can be similar. Their difference lies actually in the type of category representation, and the question of how a category actually is represented is experimentally difficult to overcome. In the following section, some examples for this problem will be described.

In animal studies, individuals are often confronted with complex stimuli such as photographs of natural scenes. D'Amato and Van Sant (1988) trained monkeys to categorize photographs depending on whether they contained a human face or not and the monkeys mastered the task (D'Amato & Van Sant, 1988). However, they showed a tendency to group certain pictures, which were not belonging to the human face category into this category. It turned out that these 'mistakes' concerned pictures sharing common characteristics with human faces (for example a half water melon being round and having a colour corresponding to that of a face). Sharing relevant features with the trained category, these stimuli were assigned to the category "human face". Results were therefore interpreted in favour of the feature theory. Stimuli used in categorization tasks may contain redundant information. As a consequence, relevant features have to acquire an influence on the animal's behaviour compared to irrelevant features. If very complex stimuli are used for the categorization (e.g. photographs of natural scenes), it is hard to tell, which features are actually used for categorization. In order to overcome the question of which features are used, some studies imply artificially generated or adapted stimuli (e.g. Huber & Lenz, 1993; Troje et al., 1999).

The exemplar theory of categorization does not imply that relevant features of a stimulus gain an associative value as compared to irrelevant ones. Here stimuli are supposed to be learned by rote, each of them gaining its associative strength, i.e. each

individual exemplar and its category membership is remembered. One problem of this theory, which is intuitive, is the amount of information that has to be stored in this case. Nevertheless, there are studies showing that at least some animals are able to learn an astonishing amount of individual instances (Vaughan & Greene, 1984). Vaughan and Greene (1984) showed that pigeons are able to learn 320 photographs by rote, which were randomly divided into two groups not following any categorical rule. This option clearly explains the categorization of familiar exemplars, but some additional mechanism is needed to explain the categorization of unfamiliar exemplars. To this end, generalization has been proposed as possibility to overcome this problem (Pearce 1988, 1991; Astley & Wasserman 1992). But here, the problem of which stimulus dimensions are used for generalization reappears. The same is true for the prototype theory. The representation of a category in terms of a prototype needs mechanisms that explain the formation of such a prototype. Once such a prototype has been formed, it is assumed to be activated whenever an exemplar is presented. The likelihood of a response to an exemplar is assumed to be related to the degree of similarity between the exemplar and the prototype. Evidence supporting these proposals comes from the fact, that exemplars with a close resemblance to a prototype are classified easier than exemplars being rather different from the prototype (Posner & Keele, 1968). For instance, humans assign a sparrow more easily to the category “bird” than a penguin, because it has a closer similarity to the generic prototype “bird”. However, this performance can easily be explained in terms of a feature extraction and evidence for this theory is hard to find in animal studies (Lea & Harrison, 1978; Pearce, 1987; Watanabe, 1988; von Fersen & Lea, 1990). A stimulus having a close resemblance with a hypothetical prototype is likely to share more features than a stimulus with greater distance.

A special case of generalization of visual stimuli concerns the perception of mirror images. Some studies show that some animals exhibit an ambiguity for mirror images of a certain visual stimulus, i.e. the original stimulus and its mirror image are confounded or the mirror image can take control of the animal's response in absence of the original stimulus (octopus: Sutherland 1969; cats: Warren 1969; rhesus monkeys: Hamilton et al. 1973; pigeons: Todrin & Blough 1983; Hollard & Delius 1982). According to this distinction, it is possible to differentiate between two kinds of mirror image ambiguity. An absolute ambiguity implies that a visual stimulus and its mirror image cannot be discriminated from each other, whereas a relative ambiguity allows discrimination but the mirror image would be preferred over other stimuli, if the original stimulus were absent. A possible explanation of this phenomenon is provided by Corballis & Beale (1970). They propose that the symmetrical structure of the nervous system is the reason for a kind of automatic neuronal transformation. However, although a mirror image is different from the original, trained stimulus, it shares nevertheless common features with it and might be categorized based on its perceptual similarity.

Studies on discrimination learning, generalization and categorization have a long tradition in experimental psychology and animal behaviour. Herrnstein (1990) concluded that categorization has “turned up at every level of the animal kingdom where it has been competently sought”. Experiments on categorization of visual stimuli have been performed with a broad variety of animals, most of them vertebrates (e. g. pigeons: Herrnstein & Loveland 1964, Greene 1983, Troje et al. 1999; chicken: Werner & Rehkämper 1999, 2001; monkeys: Schrier & Brady, 1987; chinchillas: Burdick and Miller, 1975; African grey parrot: Pepperberg, 1983; etc.). Some theories about the underlying visual object recognition strategies imply, that the processing of visual information is performed in a configural manner (e. g. Biedermann, 1987; Gauthier et al., 1998; Maurer et al., 2002;

Altmann, Bühlhoff & Kourtzi 2003). Here it is worth making an important terminological distinction to avoid confusions in the use of the word “configural”, which will appear repeatedly throughout this work. By “configural” we understand here a topographical property of a visual object, i.e. the fact that its defining visual features (or at least some of them) can be integrated into a global representation (a configuration) in which the spatial relationship between features is fundamental for defining belonging or not to a trained category. Unless it is explicitly invoked, the term configural will not be used in the sense of that corresponding to a specific learning theory (*the configural theory*) proposed for the processing of sensory compounds (Pearce, 1987; 1994). Such a theory assumes that the elements of a compound collectively enter into a single association (e.g. Pearce, 1987; 1994) such that pure elemental representations are no longer available.

As soon as recognition of an object includes more than a single feature, the spatial relationship between them, i.e. their configuration, becomes important. For example, a tree can be viewed as being composed of the crown carried by the stem, which is based on the root part. Only the specific spatial relations between the different parts of trees guarantee the recognition. Redistributing these three constitutive elements in an inappropriate spatial relationship will preclude the recognition of the resulting object as a tree. However, it remains difficult to understand which image properties are actually used in this kind of tasks. In early studies on the field of visual categorization, stimuli often were complex, using for example photographs showing a particular person or not (Herrnstein & Loveland, 1964), leading to a questionable interpretation of the results in terms of human concepts. In recent studies more weight is put on the actual parameters used for this kind of categorization (Troje et al., 1999), leading to a view that includes the animals’ point of view and referring to the fact that almost any stimulus aspect can be regarded as feature

and that features are a product of the perceiver (Fettermann, 1996; Schyns, Goldstone & Thibault, 1998).

So far, we have only focussed on conclusions and hypotheses that arose from extensive research on vertebrates. Due to the cognitive complexity of the task under study, such a research has concentrated only on a few species that are usually characterized as “efficient learners” in the experimental psychology (pigeons, monkeys, humans, etc). This narrow comparative approach has practically excluded other animal models that are useful and commonly used in understanding general principles underlying learning and memory.

The honeybee *Apis mellifera* L, constitutes a classical model for the study of cognitive capacities (Menzel & Giurfa, 2001; Giurfa, 2003; 2003a). The honeybee is a useful model not only because of its fast learning and prolonged memory capabilities but also because it offers an excellent opportunity to study the physiological basis of such capabilities (Menzel, 1985; Menzel et al., 1993; Menzel & Müller, 1996; Menzel & Giurfa, 2001; Giurfa, 2003; 2003a). Bees are floral constant, which means that they will return to a profitable food source and continue to forage on rewarding species as long as it remains profitable in terms of nectar offer and colony needs (Menzel, 1985; Waser, 1986; Chittka et al., 1999). This behaviour implies that bees not only learn the location of a food source but also that they recognise an exploited flower species and can discriminate it from other adjacent species. To this end, bees learn and memorise specific floral properties, which allow them to discriminate between rewarding and non-rewarding flowers. In this context visual information is of fundamental importance (von Frisch, 1967; Dafni et al., 1997; Giurfa & Menzel, 1997; Giurfa & Lehrer, 2001). Among the visual cues used for discrimination, shapes and patterns play an important role in close-up recognition (Wehner, 1981; Srinivasan et al., 1994; Giurfa & Menzel, 1997; Giurfa & Lehrer, 2001). Because of the relatively poor optical resolution of the insect compound eye, patterns and

shape only can drive the choice of a bee at a rather close range to the flowers (Wehner, 1981; Vorobyev et al., 1997). Nevertheless, the fact that flowers may strongly differ along these dimensions clearly indicates that these are parameters that are evaluated by bees when choosing between flowers (Menzel, 1985).

Not surprisingly, therefore, some researchers have recently oriented their attention towards the question of whether categorization phenomena can be identified in this invertebrate and if yes, which are their underlying mechanisms (see Giurfa, 2003a for review). The honeybee presents the advantage that it can easily be trained to visual stimuli presented at a feeding place and thus associated with a reward of sucrose solution. The bee will then repeatedly come back to the feeding place searching for food (von Frisch, 1967), which allows to perform experiments with an identified individual for several days (von Frisch, 1967). This allows training and testing with carefully chosen stimuli in order to perform categorization experiments in a controlled manner.

In bees early studies on visual pattern and shape recognition were performed already in the beginning of the 20<sup>th</sup> century (e. g. von Frisch, 1914; Hertz, 1933) with relatively simple stimuli (e. g. Hertz, 1933; Wehner, 1972; Gould, 1985). This is mainly due to the fact that little was known about the perceptual capacities of the insect visual system. Researchers mostly credited bees, and insects in general, with limited recognition capabilities associated with lower level cognitive abilities. The majority of studies on bee visual perception aimed towards an examination of the mechanisms of the bees visual system and only few of them asked for the implementation of such mechanisms into flexible, higher-level, cognitive strategies.

For instance, the dominant view until the eighties and even the beginning of the nineties was that bees essentially learn and recognize patterns in terms of a retinotopic template (Wehner, 1972; Gould, 1985; Ronacher & Duft, 1996). The *template* theory

postulates that patterns are perceived as a retinotopically fixed eidetic image; recognition of a perceived shape or pattern would depend on the amount of overlapping areas between a memorised representation and the actually perceived stimulus (Wehner, 1972, Gould 1985; Ronacher & Duft, 1996). The template hypothesis therefore implies a pixel-based storing and comparison of visual information. This ‘holistic’ representation is not very flexible concerning generalization and transfer of acquired information to novel, unknown stimuli (Dill et al., 1993). In fact, a small displacement of the memorised pattern in the insect visual field would preclude recognition as the retinal position of the object would be different with respect to the memorised one. This strategy is therefore extremely rigid and does not account for flexible stimuli use in the natural world, in which bees experience an enormous variety of shapes and patterns during their foraging flights and respond to the same flower species even if flowers appear differently oriented in space or are partially occluded by vegetation.

As the template theory became unsatisfactory due to its small explanatory power in numerous cases, and with progress in this research area, new experiments started to showed in the nineties that categorization of visual stimuli based on a single extracted feature is possible in honeybees. Some of these studies aimed for unrevealing the perceptual capacities and were not directly dealing with categorization (van Hateren et al., 1990; Horridge, 1997; Srinivasan et al., 1993; 1994). In fact, the term categorization is never employed in these works. Nevertheless, they have in common with other works that explicitly asked for categorization abilities in bees (Giurfa et al., 1996) that they implied training bees to a variety of stimuli sharing a common parameter and testing them with novel instances in which the common parameter trained was present. These works thus fulfilled the demands of a categorization experiment.

On the basis of these works, it was realized that flexibility of visual stimulus representation is also a property of the insects visual recognition strategies. It was therefore postulated, contrarily to the template theory, that bees extract certain characteristic isolated parameters from the patterns they perceive. This was the basis of the so-called *parameter* or *feature theory* (Giurfa et al., 1996; Srinivasan et al., 1993, 1994; Horridge and Zhang, 1995; Horridge, 1997; Horridge, 2000). Parameters which have been shown to be used as isolated cues for the categorization of novel patterns by honeybees are bilateral symmetry (Giurfa et al., 1996), orientation of edges (Srinivasan et al., 1993; 1994), radially or tangentially organised pattern elements (Horridge & Zhang; 1995; Horridge, 2000), and pattern disruption (Horridge, 1997). The extraction of a relevant parameter allows the transfer to unknown stimuli, which can vary along a broad variety of characteristics such as global shape, colour, etc., but share the common parameter that can be used for recognition. This capacity can be based on simple neural mechanisms. For example, Srinivasan et al., (1994) developed a functional model for the detection of orientations based on behavioural data from honeybees. This model assumes the existence of three theoretical broadly tuned orientation detectors, spanning over the whole visual field, each of which having a preferred orientation to which response is maximal. A perceived orientation evokes a certain activity pattern in the ensemble of these theoretical orientation detectors. Therefore, each stimulus evoking a response pattern equivalent to a previously experienced one would lead to the same response of the bee. Neuronal correlates with approximately these activation properties have been found some years later by Yang and Maddess (1997) in the medulla of the honeybee (Yang & Maddess, 1997). Similarly to these orientation detectors, filters for other parameters, such as bilateral symmetry and radial organisation of pattern elements, in the visual system of bees have been proposed (Horridge, 2000a). With the knowledge resulting from these studies, it was possible to

conceive experiments knowing which kind of features are underlying information processing.

It is worth underlining that categorization of visual stimuli by bees has been restricted up to now to the use of a single isolated feature. The possibility that insects implement configural stimulus representations, assembled from several features, has been specifically denied in several occasions (e. g. Horridge, 1996; 1997a; 2000a; 2003; 2003a). It has been argued that due to scarce cognitive power, bees cannot bind features of a visual image. This has lead to the even more surprising conclusion that bees don't perceive patterns but just react to isolated features (Horridge, 2000a; 2003; 2003a). Nevertheless, several observations contradict these statements. Horridge himself proposed in two of his earlier studies that "...bees can discriminate [...] patterns on the basis of the spatial layout of different angles of stripes." (Zhang & Horridge, 1992) and that "... bees can use the four orientations in four quadrants of the patterns..." (Horridge & Zhang, 1995), thus assuming that bees can use local orientations and their spatial relationship, when global (summed) orientation is not available as cue. A very convincing example feature binding in bees is provided by Fauria and others (Fauria et al., 2000). In this study, bees learn to prefer a radial pattern on an oblique grating (45°) background over a concentric one on the same background and the concentric pattern over the radial one, when the background grating had another orientation (135°). Like this all four elements were equally positive and negative and the task could only be solved by binding of features. Campan and Lehrer (Campan & Lehrer, 2002) propose the use of the mutual spatial relationships among different oriented edges in a discrimination of closed shapes by bees, thus also a combination of several visual elements. Therefore, there is abundant evidence, that bees are able to bind features.

In this thesis we were explicitly concerned by the possibility that bees implement configural stimulus representations for the categorization of novel complex visual images. In all experiments that we carried out, bees were trained in a dual choice situation. The apparatus was a Y-shaped maze with an entrance hole in the frontal panel through which the bees had to pass to gain access to the decision chamber. Once in the chamber, the bees could see the two stimuli being presented in the vertical plane on the back walls of the two arms of the maze. One of the stimuli was rewarded while the other was not rewarded. The position of the rewarded and the non-rewarded stimulus were interchanged in a pseudorandom way, in order to avoid learning in terms of positional cues. Thus, the training resulted in a discriminative task between the two stimuli presented. This procedure was chosen, because it has been shown, that with this kind of differential training, bees learn the global display of both stimuli, the rewarded and the non-rewarded one, and not their isolated local features (Giurfa et al., 1999). After completing the training, the bees were confronted with novel stimuli under extinction conditions (i.e. no reward available on them) in order to test their transfer capacities.

The training stimuli were circular patterns divided into four quadrants each of which contained a striped pattern (grating) with a different orientation ( $0^\circ$ ,  $45^\circ$ ,  $90^\circ$  and  $135^\circ$  with respect to the vertical). Similar patterns have been used in other studies on honeybee pattern recognition (Horridge & Zhang, 1992; Zhang & Horridge, 1995; Giurfa et al., 1999) and can be learned and discriminated by bees. The parameter orientation has been chosen, because different orientations can be combined in one pattern and allow to generate quite a large set of different transformations, which allow to address several questions concerning the categorization capacities of bees and the underlying strategies.

In this work, we studied a new alternative concerning visual categorization in bees. Up to now it was assumed that categorization of visual stimuli in bees is restricted to the

use of a single parameter (see above). The results obtained from the experiments in this study provide evidence that bees are able not only to use several stimulus elements but also to combine them in a specific spatial configuration. As already mentioned, in vertebrate studies this capacity of configural representation of complex visual stimuli has already been demonstrated. Individuals were presented with a broad spectrum of all kinds of complex stimuli, taking for granted that features are extracted, relevant features separated from irrelevant ones and spatial positions between them being learned. This kind of studies has not been conducted in bees, probably due to the scepticism about their capacity to bind different features into a global representation. From experiments partly belonging to my diploma thesis, we know that bees can generalize the information pertaining to a learned pattern towards its mirror images and left- right-transformation (permutation of the left and right sides of a pattern) if the original pattern is absent. In the Chapter I of this thesis (Stach & Giurfa, 2001) we investigated this capacity in detail and found that after a randomised training with six different patterns pairs, bees can also generalize the learned patterns to their simplified versions, as long as these preserve the appropriate spatial relationship between relevant features. Bees also preferred the left-right-transformation to the mirror image of the reduced version (Stach & Giurfa, 2001). The reasons for such preferences are analysed in the Chapter I of this thesis. In any case, the results of this first chapter led to the idea that bees might learn patterns containing several different orientations in terms of a configuration of orientations in which each retinal quadrant is associated with a specific orientation (Chapter I).

Following this reasoning I conceived experiments in order to answer the question of whether bees are actually able to combine several orientations in a specific spatial configuration and to categorize novel stimuli preserving or not this configuration (Chapter II, Stach & Giurfa, 2003). In these experiments, bees were trained like in typical

categorization experiments to a sequence of randomised pattern pairs that were all-different but shared a defined configuration of orientations. After the training was completed, the bees were presented with novel patterns preserving or not the global pattern configuration and their performance in these tests was analysed. Furthermore, I trained bees to coloured stimuli in which the receptor specific contrasts for the three receptors channels of the bees' visual system were selectively suppressed. This was done in order to identify the visual pathway implicated in this kind of task (Chapter II).

Finally, in a third chapter (Stach & Giurfa, 2003a) we analysed the influence of the training procedure on the categorization of configural patterns. A relevant question underlying the learning set principle (Harlow, 1949) in which animals are explicitly trained to solve a problem by using a unique solution or sets of solutions defined by the experimenter *a priori*, is whether the animal's natural strategy corresponds or not to the solution implemented for solving the learning set. If bees are trained to a changing sequence of patterns sharing a common configuration of orientations, they are forced to use this cue to predict the arrival of the reward of sucrose solution. Do bees categorize patterns because they are explicitly trained to do so, or does pattern categorization constitute a natural strategy that can be manifested even under simpler training forms? In order to answer this question, I studied whether a specific orientation configuration can also be used as a categorization information when bees are trained with a single pair of patterns instead of a randomly changing succession of different patterns. Moreover, I asked whether the representation of the same patterns change with increasing experience. Therefore I tested bees at different stages of the training procedure, i.e. with different levels of experience (Chapter III).

Together, we show that bees can learn a specific configuration of orientations and that different levels of experience have an important impact on the categorization

performance. These results open a large field for further investigations. The fact that in the case of orientation information bees can build configural stimulus representations leads to the question of whether this is also true for other stimulus dimensions and across different perceptual modalities. Flowers combine features belonging to different perceptual modalities. They are complex combinations of odour mixtures, colours – in many cases more than one – shape, and patterns. Can bees build across-modality configural stimulus representations? Experiments on human object recognition often use stimuli which combine their features across different modalities (e. g. Maurer et al., 2002). Such intermodal features can easily be integrated into a configural representation (Maurer et al. 2002). However, raising and answering this question in the case of bees requires careful experimental design as different sensory cues may have different perceptual salencies for honeybees (Menzel, 1985). If one element of a stimulus compound is more salient than the others it may simply overshadow the others such that learning configurations could be impaired. Depending on the visual range, bees prioritise different visual cues while approaching a floral target (Giurfa & Menzel, 1997; Giurfa & Lehrer 2001). Configural representations of floral stimuli could therefore take such a temporal component into account and link features that appear sequentially during a bee's approach flight toward a flower (Zhang et al., 1999).

The present work is organized in three chapters that correspond to three independent but nevertheless related scientific publications. In a first chapter we raise the question of whether bees can generalize their response to a mirror image and a left-right transformation of a given pattern when the trained pattern is absent. In a second chapter we asked whether bees can build configural pattern representations that could be used for stimulus categorization and identified the visual channel involved in this task. In a third chapter, we asked whether configural stimulus representations are a specific consequence

of a given training method or can also arise under simpler training forms. In asking this question we analysed the role of the cumulative experience in the visual recognition strategies used by the bees. All in all, this work presents therefore an original approach to the problem of visual stimulus categorization as it tackles the problem from the perspective of an insect. Questions about cognitive processing in insects, in this case in the visual domain, are unfortunately still seldom. The limited vision postulating that insects are just reflex machines is questioned by our findings. The picture emerging from this work is one in which bees appear as highly flexible organisms, with capacities that up to now were suspected to occur only in vertebrates. To determine precisely the performances of which the small brain of a bee is capable is certainly an important task to situate cognitive research into an appropriate comparative frame (Giurfa, 2003a). We hope that the present thesis can contribute to this end.

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