J Comp Physiol A (2013) 199:45–55
DOI 10.1007/s00359-012-0767-5

ORIGINAL PAPER

Honeybees can discriminate between Monet and Picasso paintings

**Wen Wu · Antonio M. Moreno · Jason M. Tangen ·
Judith Reinhard**

Received: 30 August 2012 / Revised: 4 October 2012 / Accepted: 4 October 2012 / Published online: 18 October 2012

Abstract Honeybees (*Apis mellifera*) have remarkable visual learning and discrimination abilities that extend beyond learning simple colours, shapes or patterns. They can discriminate landscape scenes, types of flowers, and even human faces. This suggests that in spite of their small brain, honeybees have a highly developed capacity for processing complex visual information, comparable in many respects to vertebrates. Here, we investigated whether this capacity extends to complex images that humans distinguish on the basis of artistic style: Impressionist paintings by Monet and Cubist paintings by Picasso. We show that honeybees learned to simultaneously discriminate between five different Monet and Picasso paintings, and that they do not rely on luminance, colour, or spatial frequency information for discrimination. When presented with novel paintings of the same style, the bees even demonstrated some ability to generalize. This suggests that honeybees are able to discriminate Monet paintings from Picasso ones by extracting and learning the characteristic visual information inherent in each painting style. Our study further suggests that discrimination of artistic styles is not a higher cognitive function that is unique to humans, but simply due to the capacity of animals—from insects to humans—to extract and categorize the visual characteristics of complex images.

Keywords: Honeybee · Learning · Vision · Discrimination · Generalization

Introduction

Vision is one of the most important sensory modalities for the perception of biologically relevant stimuli. It is one of the major senses of insects like honeybees, and there is abundant evidence for the honeybee's ability to quickly learn colours, shapes and patterns (von Frisch 1914, 1967; Zhang et al. 1995; Srinivasan 2010). However, simple visual cues rarely exist in nature: during their daily foraging trips, honeybees have to rely on a variety of complex visual cues from their environment in order to navigate, such as constellations of landmarks, multifaceted landscapes, and flowering trees (Collett 1996; Collett and Collett 2002; Collett et al. 2003; Steffan-Dewenter and Kuhn 2003; Dyer et al. 2008). This requires sophisticated visual processing and learning abilities. Indeed, bees have been shown to discriminate complex forest scenes (Dyer et al. 2008), be capable of categorizing images from natural scenes such as different flower shapes (Zhang et al. 2004), and most surprisingly, human faces (Dyer et al. 2005; Dyer and Vuong 2008; Avarguès-Weber et al. 2010). Furthermore, bees have been shown to display numerical processing abilities, solve delayed-matching-to-sample tasks, learn abstract rules and concepts, and transfer these to novel stimuli and tasks, even to different sensory

---

Electronic supplementary material The online version of this article (doi:10.1007/s00359-012-0767-5) contains supplementary material, which is available to authorized users.

W. Wu · J. M. Tangen
School of Psychology, The University of Queensland, Brisbane, QLD 4072, Australia

A. M. Moreno · J. Reinhard (✉)
Queensland Brain Institute, The University of Queensland, Brisbane, QLD 4072, Australia
e-mail: j.reinhard@uq.edu.au

A. M. Moreno
Department of Psychology, Federal University of Sao Carlos, Sao Carlos, SP 13560, Brazil

modalities (Srinivasan et al. 1998; Giurfa et al. 2001; Giurfa 2007; Gross et al. 2009; Avarguès-Weber et al. 2011, 2012). These are remarkable capabilities for an insect, comparable to those of vertebrates. In spite of their small brain, honeybees have the capacity to process and learn complex visual information, which in turn facilitates efficient navigation and assists foraging in their ever-changing visual environment.

Although numerous studies have demonstrated that bees can learn much more than just simple patterns, colours and shapes, the cues that honeybees use to solve complex visual tasks are still a matter of debate. Some models assume that bee vision and visual learning is determined by mechanistic hardwired circuits, and that bees rely only on low-level feature detectors and elemental cues (Horridge 2000, 2005, 2009a, b). In this scenario bees learn combinations of coinciding elemental cues as retinotopic label for a particular image and generalize between images containing similar cues. This simple elemental processing, however, cannot explain how bees use previously acquired information to solve novel tasks, categorize novel stimuli that significantly differ in low-level cues, and transfer abstract concepts to novel domains. Therefore, other models suggest that honeybee vision and visual learning is a plastic system based on multiple mechanisms (Dyer and Griffiths 2012). Depending on the visual task at hand, honeybees may rely on simple, elemental processing if sufficient, however, with increasing complexity of the task and continued visual experience, honeybees can learn to move to non-elemental processing, such as configural type processing and rule-learning, and can access top-down information to solve novel tasks (Giurfa et al. 2003; Stach et al. 2004; Stach and Giurfa 2005; Giurfa 2007; Avarguès-Weber et al. 2010; Dyer 2012).

To further investigate the cues and mechanisms underlying honeybee visual learning, we asked whether the honeybee's ability to discriminate between complex stimuli could be extended to the discrimination of paintings, which humans distinguish on the basis of artistic style—that is, Claude Monet paintings from the Impressionist period and Pablo Picasso paintings from the Cubist period. Previous work with birds has already demonstrated that the capacity for discrimination of artistic style is not limited to humans: Pigeons can learn to distinguish Monet from Picasso paintings, generalize to novel paintings by the same artist and even to paintings by other artists from the same period (Watanabe 2001; Watanabe et al. 1995). If honeybees were similarly able to distinguish multiple paintings by Monet and Picasso and then transfer this discrimination to novel paintings by the same artists, it would suggest that they are sensitive to the visual characteristics that are common to each style. With each painting being unique and differing in countless visual details from others even by the same artist, honeybees are unlikely to achieve generalization to novel paintings, if they rely only on simple elemental processing and retinotopic image matching.

Here, we investigate for the first time whether discrimination of paintings and generalization of artistic styles can be achieved by an insect that has a brain the size of a grass seed containing less than one million neurons. In a series of experiments, we tested whether honeybees could discriminate Monet from Picasso paintings at all; whether bees could learn to discriminate more than one painting pair at the same time; and whether bees could generalize their discrimination to novel paintings.

Materials and methods

Animals

Experiments used free-flying, individually marked honeybees (*Apis mellifera*) and were conducted in an indoor flight facility with controlled temperature and illumination at the Queensland Brain Institute, Australia, in accordance with the national guidelines and regulations.

General procedure

Groups of honeybees from a colony outside the facility were trained to enter the facility through a window and fly into a wooden tunnel (125 cm L × 25 cm W × 25 cm H) covered with a Perspex lid (Fig. 1). In order to exclude interactions between bees that could potentially influence a bee's choice, only one bee at a time was allowed to enter the tunnel controlled by a mesh covering the entrance. On a vertical wall at the end of the tunnel, bees were shown photographic prints (7 × 9.5 cm) of a Monet and a Picasso painting spaced 5 cm apart. Directly underneath each painting was a hole (3 × 3 cm) through which the bees could enter into chambers behind the paintings. One of the chambers contained a feeder with 1 mol sugar solution (rewarded painting); the other chamber was empty. A screen behind each entrance hole prevented bees from seeing the feeder before entering the chamber. As a result the only visual information that was available for the bees to base their choice on was the difference between the two paintings. The paintings were changed depending on the experiment that took place. After completion of the choice task, bees were released from the chambers through holes in the Perspex lid of the chambers.

Experiments

For each experiment, two groups of 25 individually marked honeybees were trained separately to discriminate between

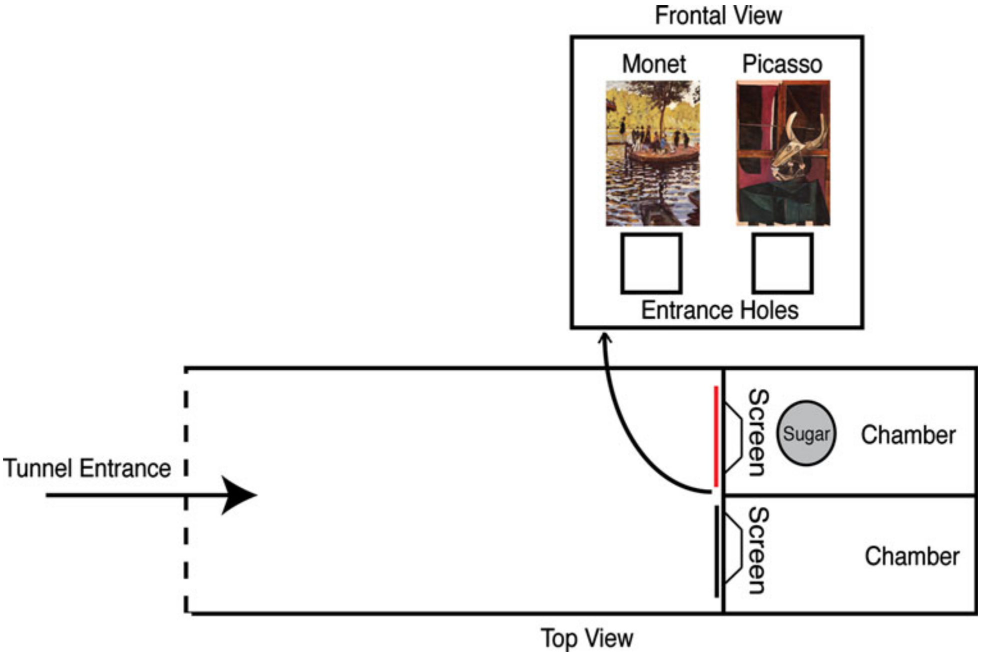

Fig. 1 Experimental tunnel investigating honeybee discrimination of Monet and Picasso paintings. Tunnel is shown from above, and placement of the Monet and Picasso paintings at a wall inside the tunnel shown from front. Bees were allowed to enter the tunnel one at a time controlled by a mesh covering the entrance. The photos of Monet and Picasso paintings were fixed 5 cm apart on a vertical wall 100 cm from the tunnel entrance. Bees could enter the chambers behind the paintings through small entrance holes underneath the paintings, to retrieve a sugar reward. A screen made of paper prevented the bees from seeing the sugar feeder in the chamber

a pair (or pairs, depending on experiment) of Monet and Picasso paintings. One group of bees was trained to Monet rewarded, the second group was trained to Picasso rewarded. Only one bee at a time was allowed to enter the tunnel, and the next bee was only allowed in once the first bee had been released from the chamber. This prevented any potential olfactory or social cues being released by a bee sitting on the feeder influencing the choice of the next bee. The feeder was exchanged for a clean feeder every 20 min (after each block, see below) to reduce the possibility of potential olfactory cues, such as pheromones deposited on the feeder that could influence the bees' choices.

Training was conducted in blocks of 20 min. To prevent side preferences, the rewarded image was presented on the right side for 10 min, then on the left side for 10 min in random order. Each bee visited the tunnel at least once, usually 3–4 times during a block, but only the bees' first choices with the rewarded image presented on the left and on the right side per block were used for analysis. The results for all bees of a group were pooled for a block, and the mean percentage of correct choices for each block (or set of five blocks, depending on experiment) was calculated. Data were analyzed using ANOVA and Fisher post hoc tests.

For the first experiment, we trained two groups of 25 bees to discriminate one Monet painting from one Picasso painting (Fig. 2a, training pair 1), with either Monet or Picasso rewarded. Training was conducted for 30 blocks over 3 days. For the second experiment, two new groups of 25 bees each were trained to discriminate between five different pairs of Monet–Picasso paintings (Fig. 2a), by showing each pair for 5 blocks per day over 5 consecutive days. For the third experiment, the same bees were trained to greyscale versions of the five Monet–Picasso pairs, using five training blocks for each pair. For the fourth experiment, the same bees were shown four unrewarded, novel Monet–Picasso painting pairs (Fig. 2b), which the bees had never encountered before. The experiment started with two blocks of rewarded training using training pair 1, then one block of the unrewarded novel pair 1, followed by two blocks of rewarded training with training pair 2, then one block of unrewarded novel pair 2, and so on, until all novel pairs had been tested, interspersed with rewarded training blocks using the familiar paintings to keep the bees motivated. The experiment was repeated with greyscale versions of the training pairs and novel painting pairs.

Stimuli

We selected the same 18 Monet and Picasso paintings used by Watanabe and colleagues in their experiment showing the pigeons' ability to discriminate between artistic styles (Watanabe et al. 1995). The images were scanned at a resolution of 1,200 dpi from various art catalogues (Gordon and Forge 1983; Rubin 1989; Poggi 1992; Stuckey 1995). A 12 pixel Gaussian blur was applied to each image and scaled to 6 % of the original size to remove the moiré patterns inherent in scanning bitmapped images. Each painting was then re-scaled so that the smaller of its height and width just filled the corresponding slide dimension, and then cropped and centred to 500 × 700 pixels. Images were organized into nine Monet and Picasso pairs in accordance to their mean luminance (Table 1) and overall colour (Fig. 2) as far as possible.

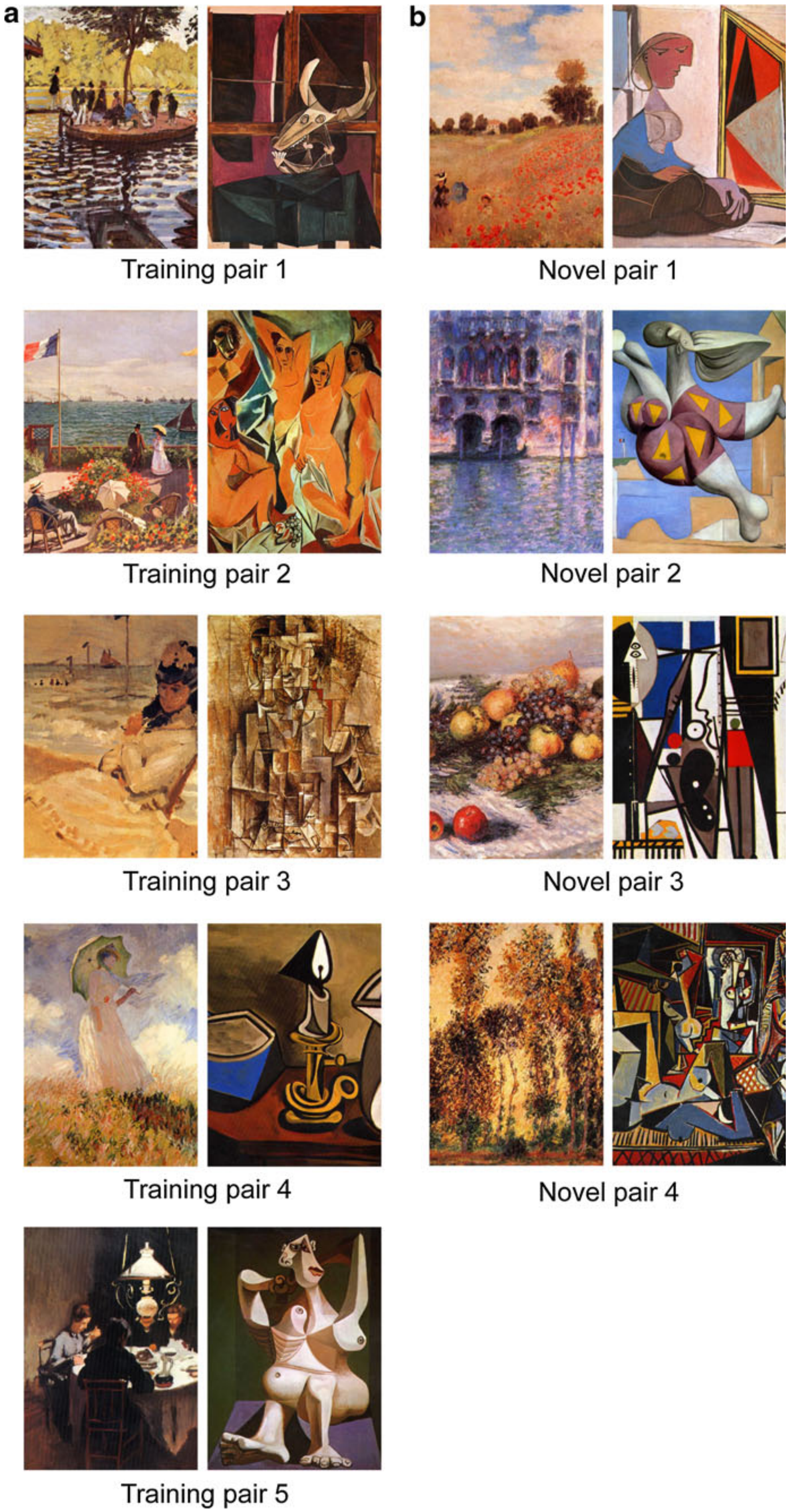

Fig. 2 Training and testing stimuli. **a** Five pairs of Monet paintings (*left*) and Picasso paintings (*right*) used for training honeybees to discriminate between the two painting styles. **b** Four pairs of Monet and Picasso paintings used to test honeybees for generalization to novel pairs after the bees had been trained to discriminate the five pairs shown under **a**. All painting pairs were matched regarding overall colour and luminance (see Table 1). Images were scanned from various art catalogues (Gordon and Forge 1983; Rubin 1989; Poggi 1992; Stuckey 1995), at a resolution of 1,200 dpi, and printed on matte photographic paper, 7 × 9.5 cm in size

Table 1 Mean luminance (lux) of the Monet and Picasso images used for discrimination training and testing for generalization to novel paintings in *Apis mellifera* honeybees

	Monet (colour)	Picasso (colour)	Monet (greyscale)	Picasso (greyscale)
Training pair 1	221	219	192	189
Training pair 2	229	233	212	215
Training pair 3	220	226	186	191
Training pair 4	224	221	205	203
Training pair 5	189	193	184	190
Novel pair 1	192	188	184	179
Novel pair 2	219	224	198	200
Novel pair 3	225	230	192	196
Novel pair 4	213	218	178	183

Images were printed on matte photographic paper 7 × 9.5 cm in size (Fig. 2), and mean luminance was measured using a digital Lux Meter (Digitech QM-1593) 15 cm in front of the images as per Zhang et al. (2004)

For example, a yellowish Monet was paired with a yellowish Picasso, or a darkish Monet was paired with a darkish Picasso (Fig. 2). Paintings were printed on matte photographic paper, 7 × 9.5 cm in size, both in colour and in greyscale. Greyscale versions of the images were slightly dimmer than the colour versions, but also had the same mean luminance (Table 1). Care was taken to ensure consistent and equal illumination on both paintings at all times during the experiments, and to avoid any reflectance, which could be used as discrimination cue by the bees.

Results

Discrimination of Monet from Picasso

When bees were trained to discriminate a Monet painting from a Picasso painting (Fig. 2a, training pair 1), both the Monet-rewarded and the Picasso-rewarded group of bees learned to discriminate between the paintings. The bees' performance measured as percentage of correct first choices increased significantly over 30 blocks of training (Fig. 3a) (ANOVA$_{\text{block effect}}$ Monet rewarded $F_{5,24} = 12.81$, $p < 0.001$; Picasso rewarded $F_{5,24} = 18.44$, $p < 0.001$). The style of painting did not affect how well bees performed, that is, bees equally discriminated the two painting styles, irrespective of whether Monet or Picasso was rewarded (ANOVA$_{\text{painting effect}}$ $F_{1,58} = 0.51$, $p = 0.477$).

Discrimination of multiple paintings

After demonstrating that honeybees are capable of discriminating a Monet painting from a Picasso painting, the next question was whether bees could extend this capacity and learn to discriminate multiple painting pairs at the same time. When presented with five different pairs of Monet and Picasso paintings (Fig. 2a), honeybees learned to discriminate all five pairs, with percentage of correct choices increasing significantly over 5 days of training for all pairs (ANOVA$_{\text{day effect}}$ Monet rewarded $F_{4,120} = 38.39$, $p < 0.001$; Picasso rewarded $F_{4,120} = 31.34$, $p < 0.001$) (Fig. 3b). There were no differences in how well bees performed over the five different training pairs (ANOVA$_{\text{pair effect}}$ Monet rewarded $F_{4,120} = 1.49$, $p < 0.208$; Picasso rewarded $F_{4,120} = 0.51$, $p < 0.725$).

Discrimination of paintings in greyscale

To investigate whether bees used colour as discrimination cue, we repeated the experiment using greyscale versions of the paintings. When the same groups of bees were presented with the greyscale versions of the five training pairs, their discrimination performance was as good as for the colour versions of the paintings, that is there was no effect of colour (ANOVA$_{\text{colour effect}}$ Monet rewarded $F_{1,48} = 2.589$, $p = 0.114$; Picasso rewarded $F_{1,48} = 1.495$, $p = 0.227$) (Fig. 3d left). Again, there was no effect of training pair (ANOVA$_{\text{pair effect}}$ Monet rewarded $F_{4,20} = 1.49$, $p = 0.244$; Picasso rewarded $F_{4,20} = 0.365$, $p = 0.831$).

Generalization to novel paintings

Lastly, we investigated whether honeybees could transfer knowledge about the visual structure that sets Monet's paintings apart from Picasso's to new images they had never encountered before. To this end, the same two groups of bees that had successfully learnt to discriminate five Monet–Picasso pairs, were shown four unrewarded, novel pairs of Monet and Picasso paintings (Fig. 2b), interspersed with blocks of rewarded training paintings (Fig. 2a). Honeybees continued to discriminate all training pairs of Monet and Picasso paintings, but did not seem to generalize to the novel pairs (Fig. 3c) (ANOVA$_{\text{pair effect}}$ Monet

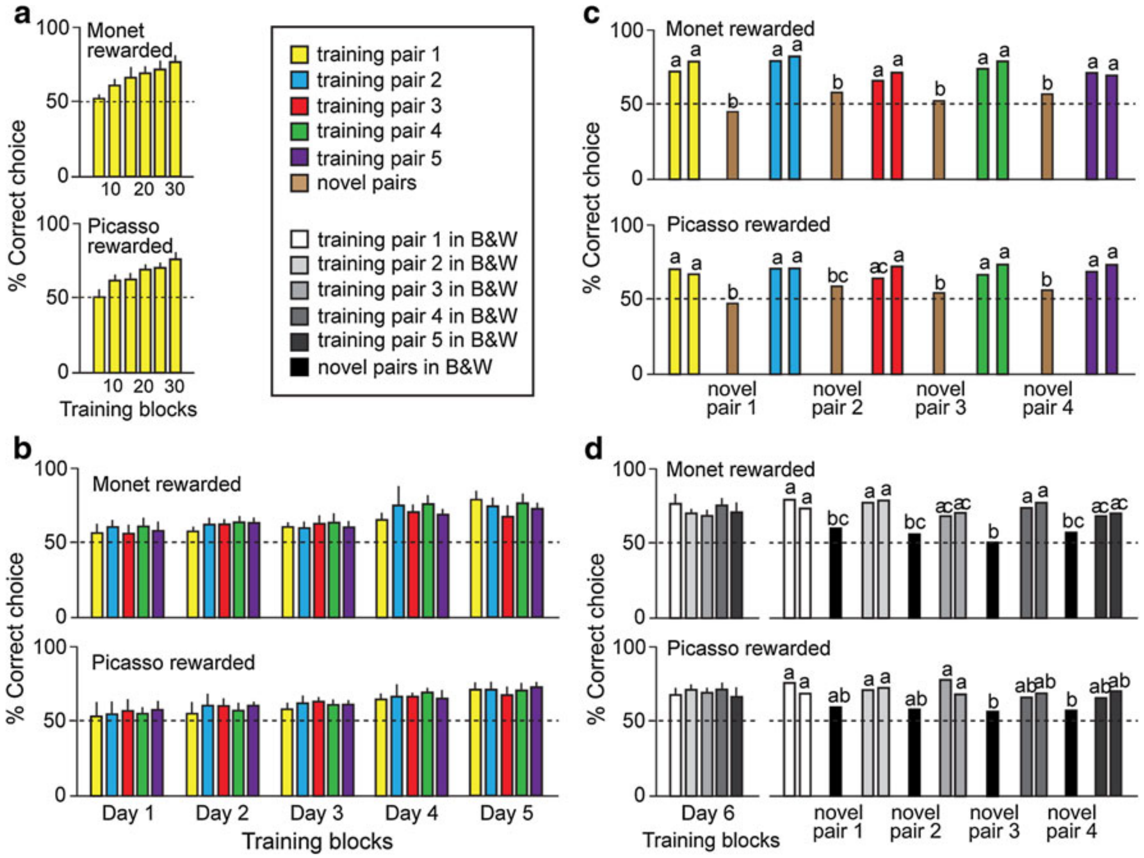

Fig. 3 Discrimination of Monet and Picasso paintings by *Apis mellifera* honeybees. **a** Percentage of correct first choices by two groups of 25 honeybees for Monet–Picasso training pair 1 (Fig. 2a). *Each bar* represents the mean ± SD of five training blocks. The bees' choices were pooled for each group. **b** Percentage of correct first choices for five Monet–Picasso training pairs. *Each bar* represents the mean ± SD of five training blocks. **c** Percentage of correct first choices for unrewarded novel pairs of Monet–Picasso paintings (Fig. 2b) interspersed by training blocks. *Each bar* represents one block. **d** *Left* percentage of correct first choices for the five different Monet–Picasso training pairs in greyscale. *Each bar* represents the mean ± SD of five blocks. *Right* percentage of correct first choices for unrewarded greyscale versions of the novel Monet–Picasso paintings interspersed by training blocks. *Each bar* represents one block. *Different letters above bars* in **c** and **d** represent statistically significant difference at $p < 0.05$ (ANOVA and Fisher post hoc test)

rewarded $F_{8,5} = 18.31$, $p < 0.003$; Picasso rewarded $F_{8,5} = 9.99$, $p < 0.011$). For the Monet rewarded group, post hoc comparisons indicated that performance for all novel pairs was significantly lower than performance for the training pairs. However, for the Picasso rewarded group, the bees' performance for novel pair 2 did not differ from training pair 3 (Fisher post hoc test; $p = 0.060$), suggesting that bees were able to generalize to novel pair 2. Notably, for both groups the percentage of correct choices for novel pairs was above chance (i.e., above 50 %) in six out of the eight tests, indicating that a weak generalization may have occurred.

We also presented the bees with novel paintings in greyscale, using the same procedure described above. Again the honeybees performed well when they discriminated the greyscale versions of the five training pairs, and their performance declined when they were presented with novel paintings (Fig. 3d, right). However, generalization to the novel pairs was better when the paintings were presented in greyscale, with only marginal or no significant difference between training pairs and most novel pairs (ANOVA$_{\text{pair effect}}$ Monet rewarded $F_{8,5} = 5.09$, $p < 0.045$; Picasso rewarded $F_{8,5} = 2.69$, $p < 0.145$). Post hoc tests revealed that for the Monet rewarded group bees' performance, for the greyscale novel pairs 1, 2, and 4, did not differ significantly from training pairs 3 and 5 (Fisher post hoc tests; range of p values 0.057–0.140). For the Picasso rewarded group, bees' performance for all novel pairs could statistically not be separated from at least two of the training pairs (Fisher post hoc test; range of p-values 0.056–0.245).

Discussion

There have been previous studies investigating how bees respond to artistic paintings, showing that naïve bumblebees are attracted to paintings displaying flowers (Chittka and Walker 2006, 2007). However, our study is the first to investigate bees' ability to discriminate and generalize between artistic styles. We show that honeybees can distinguish between Monet and Picasso paintings, and that they even learn to discriminate several painting pairs simultaneously. Considering the complexity of the paintings and the fact that these stimuli are of no biological relevance to honeybees, our results illustrate the extent of bees' visual capacities and impressive pattern recognition abilities (Gould 1985, 1986; Chittka et al. 2003; Giurfa 2007). It suggests that honeybees can learn to discriminate between many other complex images irrespective of biological relevance, and supports earlier studies showing that honeybees have the capacity to learn and distinguish multiple complex stimuli (Zhang and Srinivasan 2004; Reinhard et al. 2006; Srinivasan 2010).

What cues do honeybees use for painting discrimination?

The painting pairs were matched for luminance, where each Monet painting had similar mean luminance to its respective Picasso partner both as colour and greyscale versions. Also, the mean luminance for all pairs was in the same range, apart from training pair 5, which was slightly dimmer in the colour version (Table 1). One might argue that these measurements were based on human perceptual function and visual perception of absolute luminance between bees and humans may differ. Although bees might indeed perceive the images brighter or darker than we do, it does not change the relative measure, which demonstrates that the two images of a pair had similar mean luminance irrespective of their absolute perceived luminance. Thus, the bees would have difficulty discriminating between paintings on the basis of luminance alone.

Colour seems an obvious cue for discriminating between paintings. We therefore had matched the Monet and Picasso paintings in each pair according to their overall colour appearance—as much as possible considering the complexity of the images. However, with each painting being a unique piece of art, and therefore differing in countless colour details from its partner, the honeybees could potentially rely on specific colour cues within each painting when distinguishing one from another. Bees have the capacity to store multiple complex memories of signal combinations at any one time during their foraging trips, such as combinations of colours, scents and locations (Reinhard et al. 2006); hence it is conceivable that they might have simply memorized different colour cues and colour combinations for each individual painting and relied exclusively on this information during discrimination. However, the experiments using greyscale versions of the paintings showed that bees easily transferred their acquired knowledge from the colour pairs to the greyscale versions, therefore colour per se is not crucial for discrimination. Our findings are in line with earlier work showing that discrimination and categorization of landscapes, flowers and plant stems were not compromised when the colours of the stimuli were removed (Zhang et al. 2004).

There is the possibility that bees may use other elemental cues to discriminate Monet from Picasso paintings, such as salient edges, which bees learn very well (Horridge 2007). Monet paintings in general have less salient edges than Picasso's. However, the specific Monet images we used for this experiment all display salient edges both vertical and horizontal, particularly strong in training pairs 1, 2, and 5 (Fig. 2a). Also, considering the number and complexity of salient edges in the images, and the fact that each painting has different salient edges, it seems unlikely that bees use the complex arrangement of edges in each image as retinotopic label to identify and distinguish between the paintings.

The fact, that bees can learn to discriminate not one but several painting pairs simultaneously, indicates that bees may learn about the categorical structure of the paintings rather than the specific cues of single exemplars. This hypothesis is supported by the finding that the bees were able to generalize their discrimination to novel paintings at least to some extent.

Generalization to novel paintings

Generalization is a fundamental cognitive capacity that allows classifying or categorizing similar stimuli according to shared characteristics, treating similar stimuli as equivalents, and thus responding to them in the same manner (Zentall et al. 2008). Generalization across visual stimuli is a well-known ability in honeybees (Wehner 1971; Zhang et al. 2004; Stach et al. 2004; Lehrer and Campman 2005; Stach and Giurfa 2005; Gross et al. 2009; Horridge 2009a). It enables bees to successfully forage in an ever-changing environment, since it allows adaptive responses to novel objects. During foraging, honeybees learn the characteristics of rewarding flowers and use this knowledge not only to recognize the same flowers, but also respond to new ones with similar characteristics (Giurfa and Lehrer 2001). That is, honeybees can form categories of a type of flower or object based on a range of similar characteristics that are shared among the members of the same category. Indeed, Zhang et al. (2004) have shown that honeybees can be trained to group different naturally occurring objects, such as landscapes, plant stems and flower shapes into distinct categories, and then discriminate novel visual objects according to these categories even if the novel objects greatly differ in their individual features.

Our study showed that honeybees also discriminated some of the novel paintings they had never encountered before, although statistically the evidence for generalization was not strong. This suggests that honeybees have some ability to learn about the general visual structure that sets Monet's paintings apart from Picasso's, and generalize this knowledge to novel paintings by the same artists—in particular when the paintings are presented in greyscale. Colour may have affected the bees' ability to generalize to novel paintings, as the novel paintings differed in countless colour details from training paintings by the same artists. The new colour cues may have captured the bees' attention and distracted them from recognizing the shared characteristics. The absence of colour cues in the greyscale versions facilitated generalization to novel paintings.

The reason why generalization to novel paintings in bees was not more pronounced may lie in the training regime. Individual training length and procedure (absolute vs. differential conditioning) are known to improve discrimination and generalization of visual stimuli in honeybees, with bees moving from feature-extraction mechanisms to configural type processing with increasing experience (Giurfa et al. 2003; Stach et al. 2004; Dyer et al. 2005; Dyer and Vuong 2008; Stach and Giurfa 2005; Giurfa 2007; Avarguès-Weber et al. 2010). It is possible that a different protocol, where individual honeybees are presented with more exemplars of Monet and Picasso paintings over a longer period of time, and are tested with only one novel pair per day, would improve generalization performance to novel paintings. Indeed, similar experiments using pigeons have shown that hundreds of exemplars of a category and weeks of training are needed to achieve significant generalization to novel paintings (Watanabe et al. 1995). Due to the limited life span of insects, it is however difficult to conduct equivalent experiments in honeybees.

What cues do honeybees use for categorizing paintings?

As each painting is a unique piece of art composed of lines, shapes, edges and colours that are arranged differently, bees could not have used painting-specific information for categorization and generalization to novel paintings. Which cues then could honeybees use to characterize a 'painting style'? Honeybees are thought to use a range of stimulus features such as symmetry or orientation of objects, as well as layout of the features for categorization and generalization of visual stimuli (Stach et al. 2004; Benard et al. 2006). It is conceivable that bees learned the characteristics that are shared across the paintings of one category, such as configurations of shapes (e.g., shapes predominantly found in the image centre vs. shapes predominantly found in the image periphery vs. shapes evenly distributed across the image), orientation of objects (e.g., predominantly horizontal vs. predominantly vertical), or salient lines and edges (e.g., high load of salient edges vs. low load of salient edges). However, establishing these categories would require all Monet images used in this study to be significantly different from the Picasso images with respect to such characteristics, which was not the case (Fig. 2). Indeed, when the paintings were convoluted using horizontal and vertical filters to determine whether the majority of features and boundaries within Monet paintings compared to Picasso paintings were oriented in a particular way, we found that both artistic styles contained similar orientational information, with countless vertical, horizontal and diagonal structures in each (Online Resources 1 and 2). Due to the complexity of the paintings, there was no distinct orientational information inherent in all Picasso paintings compared to all Monet paintings, which the bees could have used as global feature for discrimination and categorization of artistic style.

Similarly, 2-D fast Fourier transforms of the paintings revealed that there is an approximately equivalent distribution of spatial frequency information in the two painting groups (Fig. 4). Although some spatial frequency spectra show slight differences when inspecting FFTs of individual painting pairs (Online Resource 3), this was not the case for all painting pairs, and the differences are too small to be used as global cue to distinguish Monet from Picasso. Hence, it is unlikely that bees use spatial frequency information for painting discrimination. Our conclusion is in line with past research for discrimination of complex forest scenes, where bees similarly could not rely on spatial frequency as cue (Dyer et al. 2008).

Clearly, further experiments are needed to determine which visual characteristics bees actually use to categorize 'painting style'. One intriguing possibility is that honeybees use the underlying visual regularities that are consistent across all paintings by the same artist. Unlike image analyses that are conducted based on the separate *individual* images (e.g., FFTs), dimension reduction techniques such as singular value decomposition (SVD) can be used to reduce the amount of symbolic information that is typically seen in images (e.g., lines, shapes and objects), but reveal the underlying dimensions that capture the most salient structural regularities *across* the entire set of Monet and Picasso paintings. Paintings reconstructed using SVD appear like amorphous colour images, but they encapsulate the most prominent visual information that is sufficient for classification (Fig. 5). There is evidence that humans rely on such underlying structural regularities when distinguishing faces (Turk and Pentland 1991; O'Toole et al. 1993; Abdi et al. 1995; Burton et al. 1999), and preliminary studies indicate that both humans and pigeons rely on structural regularities when discriminating between painting styles and between natural photographs (J. Tangen, personal communication). To test whether honeybees potentially rely on underlying structural differences between painting styles when discriminating and categorizing Monet and Picasso

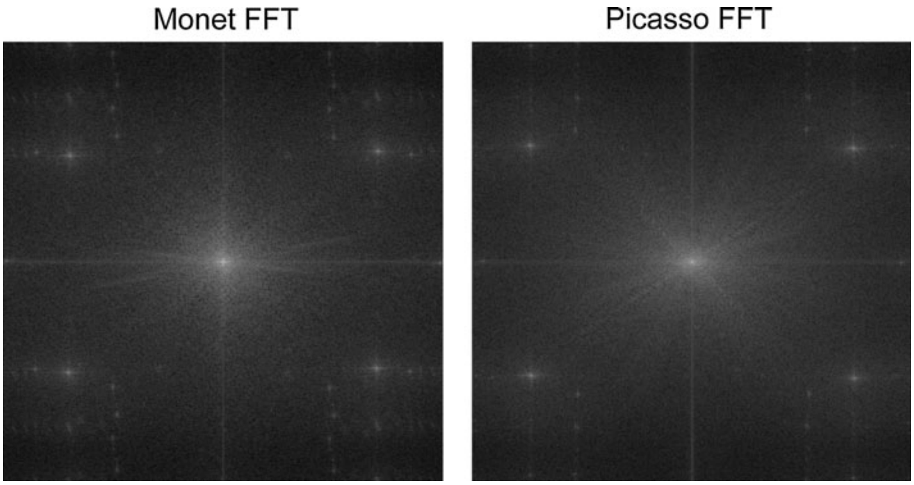

Fig. 4 2-D fast Fourier transforms (FFT) of Monet paintings (*left*) and Picasso paintings (*right*), averaged across all paintings. For FFTs of individual paintings see Online Resource 3 (Fig. S3). FFTs were carried out using Image J software. *Vertical and horizontal axes* show relative distribution of low spatial frequency information (*towards the centre*) and high spatial frequency information (*towards the edges*) in the respective images. The FFTs of Monet and Picasso paintings are very similar showing that there is an approximately equivalent distribution of spatial information in the two painting groups

Fig. 5 Examples of reconstructed paintings using singular value decomposition. *Above* two pairs of Monet and Picasso paintings in original version scanned from various art catalogues (Gordon and Forge 1983; Rubin 1989; Poggi 1992; Stuckey 1995). *Below* examples of two reconstructed Monet and Picasso painting pairs based on covariance information. Dimension reduction and reconstruction was achieved using singular value decomposition (SVD). Reconstructed images reflect the 10 primary dimensions (eigenvectors) that most strongly differentiate Monet from Picasso across a set of 160 Picasso and 160 Monet paintings

paintings, we would have to train them with dozens of different painting pairs, both with original and reconstructed images, over an extended period of time. Unfortunately, as mentioned above, such lengthy training regimes are very difficult with honeybees—at least with this species.

Conclusions

Our study does not yet provide a conclusive explanation of how bees solve the task of discriminating and categorizing complex images. Based on our data, however, we can assume that honeybees do not rely on particular elemental features such as luminance, colour, salient edges, orientation or spatial frequency content. It is more likely that they use feature extraction and/or configural processing to learn the visual characteristics that are shared across the paintings of one category, which is consistent with the way honeybees are thought to process human faces, forest scenes and landscapes, and solve novel visual tasks (Stach et al. 2004; Zhang et al. 2004; Stach and Giurfa 2005; Dyer et al. 2005, 2008; Dyer and Vuong 2008; Avarguès-Weber et al. 2010). Thus, our study contributes to the growing body of evidence that insects like honeybees have the ability to learn, retain, classify and process visual information in a way that is not predicted by simple mechanistic or elemental responses to stimuli (Dyer 2012). Of course, the fact that bees can discriminate paintings does not imply that bees actually recognize an artistic style per se or interpret art content at a semantic level in a similar way to humans. But it suggests that discrimination of artistic styles is not a higher cognitive function that is unique to humans, but may simply be due to the capacity of animals, from insects to humans, to extract and categorize the visual characteristics of complex images. The fact that bees (or pigeons) can distinguish art is surprising only to the extent that one believes their discriminations are based on local elemental features *within* each painting. Artistic style, however, is based on information that is shared *across* paintings. Future work will show whether bees are indeed sensitive to redundant visual information that is consistent across several images, which is captured by covariance measures such as SVD.

Acknowledgments We thank Chin Y. J. Yuen for help with the experiments, and Adrian Dyer and Allen Cheung for advice on the image analyses. W.W. was funded through an Australian Postgraduate Award by the Australian Government and an Australian Research Council Discovery grant to JT (DP0985830). A.M.M. was funded by a FAPESP doctorate scholarship (08/50576-8), Brazil.

References

Abdi H, Valentin D, Edelman B, O'Toole AJ (1995) More about the difference between men and women: evidence from linear neural networks and the principal component approach. Percept 24:539–562

Avarguès-Weber A, Portelli G, Benard J, Dyer AG, Giurfa M (2010) Configural processing enables discrimination and categorization of face-like stimuli in honeybees. J Exp Biol 213: 593–601

Avarguès-Weber A, Deisig N, Giurfa M (2011) Visual cognition in social insects. Annu Rev Entomol 56:423–443

Avarguès-Weber A, Dyer AG, Combe M, Giurfa M (2012) Simultaneous mastering of two abstract concepts by the miniature brain of bees. PNAS 109:7481–7486

Benard J, Stach S, Giurfa M (2006) Categorization of visual stimuli in the honeybee *Apis mellifera*. Anim Cogn 9:257–270

Burton AM, Bruce V, Hancock PJB (1999) From pixels to people: a model of familiar face recognition. Cogn Sci 23:1–31

Chittka L, Walker J (2006) Do bees like Van Gogh's sunflowers? Optics Laser Technol 38:323–328

Chittka L, Walker J (2007) Insects as art lovers: bees for Van Gogh. Antennae 2:37–42

Chittka L, Dyer AG, Bock F, Dornhaus A (2003) Bees trade off foraging speed for accuracy. Nature 424:388

Collett TS (1996) Insect navigation en route to the goal—multiple strategies for the use of landmarks. J Exp Biol 199:227–235

Collett TS, Collett M (2002) Memory use in insect visual navigation. Nat Rev Neurosci 3:542–552

Collett TS, Graham P, Durier V (2003) Route learning by insects. Curr Opin Neurobiol 13:718–725

Dyer AG (2012) The mysterious cognitive abilities of bees: why models of visual processing need to consider experience and individual differences in animal performance. J Exp Biol 215:387–395

Dyer AG, Griffiths DW (2012) Seeing near and seeing far: behavioural evidence for dual mechanisms of pattern vision in the honeybee (*Apis mellifera*). J Exp Biol 215:397–404

Dyer AG, Vuong QC (2008) Insect brains use image interpolation mechanisms to recognise rotated objects. PLoS ONE 3:e4086

Dyer AG, Neumeyer C, Chittka L (2005) Honeybee (*Apis mellifera*) vision can discriminate between and recognise images of human faces. J Exp Biol 208:4709–4714

Dyer AG, Rosa MGP, Reser DH (2008) Honeybees can recognise images of complex natural scenes for use as potential landmarks. J Exp Biol 211:1180–1186

Giurfa M (2007) Behavioral and neural analysis of associative learning in the honeybee: a taste from the magic well. J Comp Physiol A 193:801–824

Giurfa M, Lehrer M (2001) Honeybee vision and floral displays: from detection to close-up recognition. In: Chittka L, Thomson JD (eds) Cognitive ecology of pollination. Cambridge University Press, Cambridge, pp 61–82

Giurfa M, Zhang SW, Jenett A, Menzel R, Srinivasan MV (2001) The concepts of 'sameness' and 'difference' in an insect. Nature 410:930–933

Giurfa M, Schubert M, Reisenman C, Gerber B, Lachnit H (2003) The effect of cumulative experience on the use of elemental and configural visual discrimination strategies in honeybees. Behav Brain Res 145:161–169

Gordon R, Forge A (1983) Monet. Abrams, New York

Gould JL (1985) How bees remember flower shapes. Science 227:1492–1494

Gould JL (1986) Pattern learning by honeybees. Anim Behav 34:990–997

Gross HJ, Pahl M, Si A, Zhu H, Tautz J, Zhang SW (2009) Number-based visual generalisation in the honeybee. PLoS ONE 4:e4263

Horridge A (2000) Seven experiments on pattern vision of the honeybee, with a model. Vision Res 40:2589–2603

Horridge A (2005) What the honeybee sees: a review of the recognition system of *Apis mellifera*. Physiol Entomol 30:2–13

Horridge A (2007) The preferences of the honeybee (*Apis mellifera*) for different visual cues during the learning process. J Insect Physiol 53:877–889

Horridge A (2009a) Generalization in visual recognition by the honeybee (*Apis mellifera*): a review and explanation. J Insect Physiol 55:499–511

Horridge A (2009b) What does an insect see? J Exp Biol 212: 2721–2729

Lehrer M, Campan R (2005) Generalization of convex shapes by bees: what are shapes made of? J Exp Biol 208:3233–3247

O'Toole AJ, Abdi H, Deffenbacher K, Valentin D (1993) Low-dimensional representation of faces in higher dimensions of face space. J Opt Soc Am 10:405–411

Poggi C (1992) In defiance of painting: cubism, futurism and the invention of collage. Yale University Press, New Haven Connecticut

Reinhard J, Srinivasan MV, Zhang SW (2006) Complex memories in honeybees: can there be more than two? J Comp Physiol A 192:409–416

Rubin WS (1989) Picasso and Braque: pioneering cubism. Museum of Modern Art, New York

Srinivasan MV (2010) Honey bees as a model for vision, perception, and cognition. Annu Rev Entomol 55:184–267

Srinivasan MV, Zhang SW, Zhu H (1998) Honeybees link sights to smells. Nature 396:637–638

Stach S, Giurfa M (2005) The influence of training length on generalization of visual feature assemblies in honeybees. Behav Brain Res 161:8–17

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

Steffan-Dewenter I, Kuhn A (2003) Honeybee foraging in differentially structured landscapes. Proc R Soc Lond B 270:569–575

Stuckey CF (1995) Claude Monet 1840–1926. Thames and Hudson, New York

Turk M, Pentland A (1991) Eigenfaces for recognition. J Cogn Neurosci 3:71–86

von Frisch K (1914) Der Farbensinn und Formensinn der Biene. Zool Jb Physiol 37:1–238

von Frisch K (1967) The dance language and orientation of bees. Belknap Press, Cambridge

Watanabe S (2001) Van Gogh, Chagall and pigeons: picture discrimination in pigeons and humans. Anim Cogn 4:147–151

Watanabe S, Sakamoto J, Wakita M (1995) Pigeon's discrimination of paintings by Monet and Picasso. J Exp Anal Beh 63:165–174

Wehner R (1971) The generalization of directional visual stimuli in the honey bee, *Apis mellifera*. J Insect Physiol 7:1579–1591

Zentall T, Wasserman EA, Lazareva OF, Thompson R, Ratterman MJ (2008) Concept learning in animals. Comp Cogn Behav Rev 3:13–45

Zhang SW, Srinivasan MV (2004) Exploration of cognitive capacity in honeybees: higher functions emerge from a small brain. In: Prete FR (ed) Complex worlds from simpler nervous systems. MIT Press, Cambridge, pp 41–74

Zhang SW, Srinivasan MV, Collett TS (1995) Convergent processing in honeybee vision: multiple channels for the recognition of shape. PNAS 92:3029–3031

Zhang SW, Srinivasan MV, Zhu H, Wong J (2004) Grouping of visual objects by honeybees. J Exp Biol 207:3289–3298