

Honeybee (*Apis mellifera*) vision can discriminate between and recognise images of human faces

Adrian G. Dyer^{1,2,*}, Christa Neumeyer¹ and Lars Chittka³

¹*Institut für Zoologie III (Neurobiologie), Johannes Gutenberg Universität, Mainz, 55099, Germany*, ²*Clinical Vision Sciences, La Trobe University, Victoria 3086, Australia* and ³*School of Biological Sciences, Queen Mary, University of London, London, E1 4NS, UK*

*Author for correspondence at present address: Department of Plant Sciences, University of Cambridge, Downing Street, Cambridge, CB2 3EA, UK (e-mail: a.dyer@latrobe.edu.au)

Accepted 13 October 2005

Summary

Recognising individuals using facial cues is an important ability. There is evidence that the mammalian brain may have specialised neural circuitry for face recognition tasks, although some recent work questions these findings. Thus, to understand if recognising human faces does require species-specific neural processing, it is important to know if non-human animals might be able to solve this difficult spatial task. Honeybees (*Apis mellifera*) were tested to evaluate whether an animal with no evolutionary history for discriminating between humanoid faces may be able to learn this task. Using differential conditioning, individual bees were trained to visit target

face stimuli and to avoid similar distractor stimuli from a standard face recognition test used in human psychology. Performance was evaluated in non-rewarded trials and bees discriminated the target face from a similar distractor with greater than 80% accuracy. When novel distractors were used, bees also demonstrated a high level of choices for the target face, indicating an ability for face recognition. When the stimuli were rotated by 180° there was a large drop in performance, indicating a possible disruption to configural type visual processing.

Key words: visual processing, face recognition, honeybee, brain.

Introduction

There is considerable interest in the mechanisms that facilitate recognition of human faces (Bruce, 1988; Kanwisher, 2000; Tarr and Cheng, 2003; Duchaine et al., 2004). It has been suggested that the human brain may have specialised regions to allow for the processing of faces (Kanwisher et al., 1997; Kanwisher, 2000; Duchaine et al., 2004). For example, using fMRI imaging techniques, the fusiform gyrus region of the human brain shows increased activity when human subjects view face images but not control images such as other animals (Kanwisher et al., 1997; Kanwisher, 2000). It has also been observed that human subjects show a disproportionate deficit for recognising faces when a stimulus is rotated by 180° (Yin, 1969; Bartlett and Searcy, 1993; Campbell et al., 1997; Pascalis et al., 2002; Duchaine et al., 2004). Furthermore, subjects suffering a condition known as prosopagnosia, which is a severe deficit in recognising faces, are reported to have normal processing of other classes of objects, such as artificial, computer-generated creatures called ‘greebles’ (Duchaine et al., 2004). The apparent specialised ability of the human brain for recognising the faces of conspecifics has been suggested as being important to the complex social interactions of humans (Pierce et al., 2001).

The evidence for a special region of the human brain for processing faces has recently been challenged, however, by

data showing that the fusiform gyrus in subjects who have a particular field of expertise, for example bird watchers or car experts, also shows increased activity when these subjects view stimuli from their specific class of expertise (Gauthier et al., 2000; Tarr and Gauthier, 2000). In addition, a fMRI study of subjects with autism shows that face processing can be reliably facilitated by regions of the brain other than the fusiform gyrus (Pierce et al., 2001).

Other animals, including invertebrates, are able to recognise conspecifics using facial cues (Kendrick et al., 2001; Tibbetts, 2002; Tibbetts and Dale, 2004). For example, individual paper wasps (*Polistes fuscatus*) are able to recognise the facial features of other individual wasps to help maintain a strong social order within a hive (Tibbetts, 2002). However, even in humans it is currently not clear whether face recognition requires specialised, species-specific neuronal circuitry, or if face recognition might be a learned expertise, as a result of extensive experience with a certain class of visual stimuli (Tarr and Cheng, 2003). In the present study, the honeybee (*Apis mellifera*) was used as an animal model that has not been exposed to evolutionary pressure for recognising human faces but does have impressive pattern recognition and cognitive abilities that might facilitate the task (Gould, 1985; Lehrer, 1997; Chittka et al., 2003; Stach et al., 2004; Dyer and Chittka,

2004; Zhang and Srinivasan, 2004). For example, there is evidence that bees may solve visual tasks using either configural retinotopic-template type matching strategies (Wehner, 1981; Gould, 1985, 1986; Srinivasan, 1994; Giger and Srinivasan, 1995) and/or a set of features extracted from stimuli (Srinivasan, 1994; Giger and Srinivasan, 1995; Efler and Ronacher, 2000; Stach et al., 2004). If bees can recognise human faces, then this is evidence that face recognition requires neither a specialised neuronal circuitry nor a fundamentally advanced nervous system.

Materials and methods

Honeybee experiments

Honeybees were maintained in a colony located 25 m from a feeding site where foragers collected 10% sucrose solution. Individual foragers were captured at the feeding site and transferred 5 m to a test site. At the test site, a bee was colour marked and given 25% sucrose solution.

Stimuli were 6×8 cm achromatic photographs presented on a vertical, circular plastic screen of 50 cm diameter that could be rotated to prevent position learning (Fig. 1A). Two target and two distractor stimuli were mounted on freely rotating hangers with a landing platform (Fig. 1B). The experiment allowed the bees to fly towards a stimulus and choose the visual angle required to solve the task (Lehrer, 1993; Giger and Srinivasan, 1995; Horridge, 1996; Efler and Ronacher, 2000). A target stimulus contained a reward of a 10 µl drop of 25% sucrose solution and a distractor stimulus contained a punishment of a 10 µl drop of 0.12% quinine hemisulphate to promote motivation to perform difficult visual discrimination tasks (Chittka et al., 2003).

Bees were given pre-training to a simple discrimination task of a target face taken from a standard face recognition test (Warrington, 1996a) and a computer-generated schematic distractor (Fig. 1C, column i). The stimuli were cropped to exclude spatial cues such as clothing in the original images enabling recognition (Fig. 1). Bees collected sucrose solution until satiated, at which point they returned to the hive, and this set of actions was defined as a foraging bout. Between bouts, landing platforms and stimuli were cleaned with 30% ethanol. The pre-training stage allowed bees to learn that they would receive rewards for correct decisions and punishment for incorrect decisions, analogous to how human subjects gain experience with stimuli and apparatus for a psychophysics type experiment (Maddox and Bohil, 2004). When a bee landed on the platform of a target stimulus, it drank the sucrose solution, and then an additional drop was presented on a clear Plexiglas spoon so that the bee could be moved 1 m away from the screen. Whilst the bee was drinking the sucrose solution on the spoon, its body position was rotated so that it was looking away from the stimuli, and during this time stimuli positions were altered to prevent bees associating rewards with particular spatial locations. When a bee had consumed the sucrose solution on the spoon it then approached stimuli again and had to learn the correct stimulus

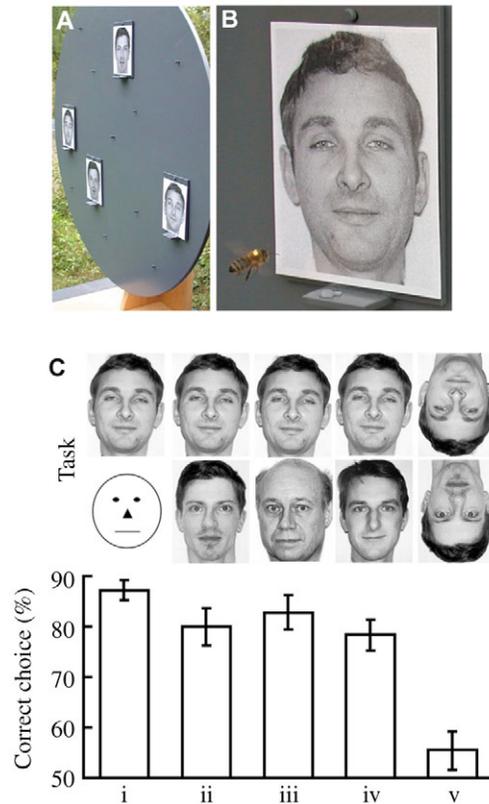


Fig. 1 (A) Foraging set up for honeybees. (B) Bee looking at a target face. (C) The ability of bees to discriminate between images of human faces. The upper region shows task (target top and distracter bottom), and the column immediately below shows mean percentage of correct choices for five bees in non-rewarded tests (± 1 S.E.M.). Bees were trained to the face at the top of column i versus a schematic face distracter, then to recognise the target face from the distracter in column ii. Bees then recognised the target face from novel distracters (columns iii, iv) but failed to discriminate faces rotated by 180° (column v). Pooled choices for non-rewarded tests in the respective conditions (i=166, ii=246, iii=199, iv=196, v=141).

in order to collect rewards. The procedure of moving the bees away from the screen during training was important as this prevented bees from simply flying vertically between the landing platforms without visually inspecting a stimulus. Pilot experiments indicated that bees did not learn even the simple pre-training task well unless they were taught to first horizontally approach the stimuli from a distance. Five bees learned this pre-training task well and were subsequently trained with face stimuli (see below). Two other bees failed to show any indication of learning even the relatively simple pre-training task as they usually flew to the high contrast contours of the schematic face; these two bees subsequently received the quinine hemisulphate solution on a majority of visits to stimuli and soon lost interest in the experiment and did not return to the testing site. The results reported in this study thus represent data for bees that were highly trained to the visual task. In a given bout, the mean (\pm S.E.M.) number of choices by the bees was 10.0 ± 1.7 . When acquisition

reached above 80% correct choices, the bees were given a non-rewarded test.

The task was then changed by presenting distractor face stimuli that were similar to the target stimuli (Fig. 1C, column ii). The bees were trained with differential conditioning (Giurfa et al., 1999; Dyer and Chittka, 2004), and when acquisition reached 80% (10 training bouts) each bee was tested in a non-rewarded trial that terminated when the test bee first lost interest in making choices and temporarily abandoned the test apparatus. Distractor stimuli were then removed from the screen, and a drop of sucrose solution was placed on the target stimuli. When the bee subsequently returned it was allowed to collect sucrose from the target stimuli until satiated to ensure motivation for additional non-rewarded trials.

Each bee was then presented with non-rewarded tests using the target stimuli and two different types of novel distractor stimuli (Fig. 1C, columns iii and iv, respectively). These two tests were done sequentially, and between these tests bees were rewarded to ensure motivation.

Bees were then given a non-rewarded test using the original training face stimuli where both of these stimuli were rotated by 180° (Fig. 1C, column v). The entire sequence of tests was completed in one day for each of five bees.

Finally, two of the bees were given a non-rewarded test with original training stimuli two days after their initial training to evaluate whether the learning of face stimuli had led to formation of a long-term memory.

Human subject subjective rankings of faces

Six human subjects (mean age \pm S.E.M., 27.8 ± 2.2 years) with normal corrected vision were asked to rank the three distractor face stimuli in relation to the perceptual similarity to the target face stimulus. This was done by simultaneously presenting the target stimulus and the three different distractor stimuli and individually asking each subject to rank the distractor stimuli faces in order of similarity to the target stimulus. It is known that the adult human visual system recognises faces mainly by using a configural strategy (Tanaka and Farah, 1993; Bartlett and Searcy, 1993; Tanaka and Sengco, 1997; Collishaw and Hole, 2000). The subjective rankings were determined to investigate if bee choices for the different distractor faces correlated with how humans ranked the perceptual similarity of distractor stimuli.

Results

After each bee was trained to the target face *versus* the schematic distractor stimuli for over 50 visits, their ability to discriminate stimuli was tested in non-rewarded trials, and choices were significantly different from chance (Fig. 1C, column i; $\chi^2=98.1$, d.f.=1, $P<0.001$). Fig. 2 shows that, when the distractor face stimulus was introduced into the test scenario, the frequency of correct choices was initially close to the 50% random foraging line, showing that, despite the pre-training with the target face, the bees were not yet able to discriminate the target face from a similar distractor. However,

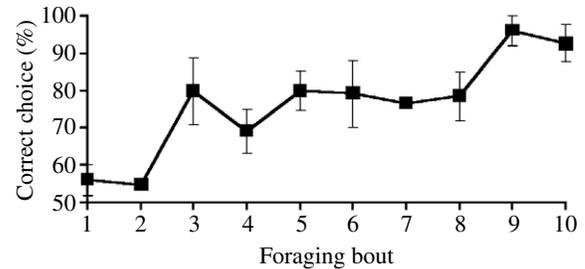


Fig. 2. Acquisition for five bees (\pm S.E.M.) learning to discriminate a target face from the distractor face stimulus shown in Fig. 1C column ii.

with continued differential conditioning (Giurfa et al., 1999; Dyer and Chittka, 2004) the bees gradually learned to discriminate between the similar human face stimuli (Fig. 2).

Following differential conditioning, correct choices for the target face were evaluated in a non-rewarded test (Fig. 1C, column ii). During both training and the non-rewarded tests, the bees often hovered in front of a stimulus before making a decision to land (Fig. 1B), and the mean hovering distance from the stimuli was 6.4 ± 1.1 cm (S.E.M.). The choices for the target face were significantly different from chance ($\chi^2=94.8$, d.f.=1, $P<0.001$), showing that it is possible for this animal model to learn how to discriminate between images of human faces. Correct choices for the target face *versus* the novel distractors were also significantly different from chance ($\chi^2=141.5$, d.f.=1, $P<0.001$), indicating that, in addition to being able to discriminate a target face from a learned distractor, bees were able to recognise the target face from novel distractors.

Bees tested on the original training pair of faces, but with both faces rotated by 180° (Fig. 1C, column v), performed significantly poorer (Wilcoxon Signed Rank Test; $N=5$, $Z=-2.023$, $P=0.043$), indicating that stimulus rotation disrupts the bees' ability to process the learned images of the faces.

Two bees tested 2 days after the initial training retained the information in long-term memory. One bee scored 93.9% on the initial day of training and 79.2% 2 days later; and a second bee achieved scores of 87.4% and 75.9%, respectively. This shows that the differential conditioning to face stimuli led to the formation of a long-term memory in bees.

Human subject subjective rankings of faces

All six subjects ranked distractor faces in the same order; compared with target, the most similar face was the distractor in Fig. 1C column iv, the distractor in column ii was ranked second and the least similar face was the distractor in column iii. The ranking of the three distractor face stimuli in relation to the perceptual similarity of the target face stimulus by human subjects was tested for a correlation with how accurately the bees discriminated between stimuli. Whilst the bees choices shown in Fig. 1C indicate a trend that bees do discriminate between faces more accurately when the faces are ranked perceptually less similar by humans, this relationship was not significant ($r_s=0.151$, $N=15$, $P=0.591$).

Discussion

The findings of this study show that honeybees have the ability to both discriminate between target and distractor faces that have been learned (Fig. 1C, column ii) and to recognise the target face from novel distractors (Fig. 1C, columns iii and iv). The level of recognition is impressive considering that the stimuli used for the experiments were taken from a standard face-recognition test for which human subjects experience a reasonable degree of difficulty (Warrington, 1996a,b). We ascribe the high level of performance to four important components of the training procedure: (1) bees were first given pre-training to a relatively simple discrimination task, which enabled them to learn that there was a task to be solved; (2) bees were punished for errors with a bitter-tasting solution that has the effect of increasing bee motivation to solving difficult tasks (Chittka et al., 2003); (3) bees were provided with extensive amounts of differential conditioning (Giurfa et al., 1999) to the training stimuli to allow a sufficient time to be able to learn the visual task; (4) stimuli were presented with an unconstrained visual angle that allowed bees to potentially use either configural and/or feature extraction visual strategies (Efler and Ronacher, 2000).

Two possible mechanisms by which bees may process spatial information are either by using a retinotopic-template type matching strategy or by using a set of features extracted from the stimuli (Efler and Ronacher, 2000). There is evidence that in some circumstances bees use retinotopic-template type matching that is consistent with configural processing (Wehner, 1981; Gould, 1985; Gould, 1986; Srinivasan, 1994; Giger and Srinivasan, 1995), whilst in some circumstances the data are more consistent with a feature extraction model of visual processing (Srinivasan, 1994; Giger and Srinivasan, 1995; Efler and Ronacher, 2000; Stach et al., 2004). For face recognition tasks, adult humans mainly use a configural visual strategy (Tanaka and Farah, 1993; Bartlett and Searcy, 1993; Tanaka and Sengco, 1997; Collishaw and Hole, 2000). Bee choices for the different faces were not significantly correlated with adult human perceptual rankings for faces, possibly suggesting bees were not using a configural strategy to solve the task. However, a confounding factor is that in human processing of faces, subjects develop different visual strategies between the ages of 6 and 10 years; at 6 years of age children appear to use a feature extraction model of visual processing but by 10 years of age performance is more consistent with a configural model of visual processing (Carey and Diamond, 1977) and it is also known that bees do use different visual strategies depending upon the type and level of conditioning to spatial features (Giurfa et al., 2003). Furthermore, recent work using eye movement studies in humans suggests that whilst adults use a configural mechanism to recognize faces, the learning of faces by humans requires some level of feature extraction processing to promote reliable recognition (Henderson et al., 2005). The absence of a relationship between bee choices and adult human perceptual rankings could thus be a result of either (1) the extent to which bees were using configural processing not

being as strong as in adult humans who have had much more extensive experience with faces or (2) bees solving the task using a feature extraction model of visual processing. In the former, bees may move from feature extraction to configural processing depending upon their individual level of experience.

Stach et al. (2004) show that bees are able to link and assemble local features of a visual pattern to construct a representation of a stimulus, suggesting that some form of a feature extraction model may enable bees to solve the face recognition task. However, the large decrease in the frequency of bee correct choices when the stimuli were rotated by 180° suggests that configural processing may have been disrupted, since this type of stimulus manipulation has a much greater effect on configural rather than feature extraction mechanisms in human visual processing of face stimuli (Collishaw and Hole, 2000). Thus, from the data in the current experiments, it is not possible to definitively conclude which mechanism bees use to recognise images of human faces, which indeed may be because individual bees might use different mechanisms depending upon the level of experience with the training stimuli (Giurfa et al., 2003). Future experiments may be able to reveal the visual mechanism used by bees to facilitate face recognition by using a wider range of face stimuli and by considering the variety of approaches previously used to reveal feature extraction and configural mechanisms for the human perception of faces (e.g. Yin, 1969; Carey and Diamond, 1977; Bruce, 1988; Rizzo et al., 1987; Tanaka and Farah, 1993; Tanaka and Sengco, 1997; Collishaw and Hole, 2000).

The honeybee brain has less than 0.01% the number of neurons of the human brain (Zhang and Srinivasan, 2004). There has been considerable debate about the level of cognitive resources required to recognise faces. Some evidence suggests that highly specialised neural regions within the mammalian brain are required for face recognition tasks (Kanwisher et al., 1997; Kanwisher, 2000), whilst other studies suggest that face recognition is only one case of visual expertise with a certain class of stimuli (Gauthier et al., 2000; Tarr and Gauthier, 2000; Tarr and Cheng, 2003). Pascalis et al. (2002) tested the visual capabilities of 6-month-old and 9-month-old human infants and showed that the six-month-old infants were equally good at recognising both human and non-human primates, whilst by 9 months of age the perceptual window narrows towards recognising individuals within the human species. However, this neural plasticity in humans appears to be confined to face categories that include human and primate faces but not faces from a totally different species such as cows (Campbell et al., 1997). Many hymenopteran insects have impressive cognitive abilities that are used to detect and identify different types of flowers in order to collect nutritional rewards (Gould, 1985; Lehrer, 1997; Chittka et al., 2003; Stach et al., 2004; Dyer and Chittka, 2004; Zhang and Srinivasan, 2004). The studies by Tibbetts (2002) and Tibbetts and Dale (2004) show that hymenopteran insects are capable of recognising the faces of conspecifics in the context of complex social structures, but to our knowledge this current study is the first report that

invertebrates have sufficient neural flexibility to learn how to discriminate between and recognise faces of other species.

In normal human subjects, the processing by the visual and neural system for faces is very fast (Campbell et al., 1997; Pascalis et al., 2002) and can deal with a large number of different faces (Standing et al., 1970; Bruce, 1988). Whilst an insect's brain is unlikely to be able to reach these levels of performance, our results show that recognition of human faces can be achieved by a honeybee brain following differential conditioning to this class of visual stimuli. This suggests that face recognition is a task that can be solved, at least to a certain level, by a general neural system that has a reasonable degree of plasticity. The finding that bees can reliably recognise faces may seem surprising in the context that there are human subjects who suffer from prosopagnosia and are unable to recognise the faces of familiar persons, despite having reasonably normal visual processing (Rizzo et al., 1987; De Renzi and di Pellegrino, 1998; Duchaine, 2004). However, there is evidence that subjects with prosopagnosia may covertly recognise individual faces and that the inability to be able to report recognition is due to limitations on the activation of associated memory for a face (Tranel and Damasio, 1985), even though the visual system has captured sufficient information to allow for a recognition (Tranel and Damasio, 1985; Rizzo et al., 1987). The results in this current study show that even bees are capable of recognising human faces and thus supports the view that the human brain may not need to have a visual area specific for the recognition of faces (Gauthier et al., 2000; Tarr and Gauthier, 2000; Tarr and Cheng, 2003). However, the result cannot fully exclude the possibility that the human brain does have a specific region for the processing of faces since there is also evidence from one subject for whom face processing remains normal despite agnosia (a recognition deficit) for non-face objects (Moscovitch et al., 1997). Further experiments with bees that tackle fundamental questions that have been investigated in humans for face recognition tasks (Yin, 1969; Carey and Diamond, 1977; Bruce, 1988; Rizzo et al., 1987; Tanaka and Farah, 1993; Tanaka and Sengco, 1997; Collishaw and Hole, 2000) may reveal the extent to which a relatively simple brain can solve these tasks and may thus help define a baseline for the minimum cognitive resources required to facilitate face recognition.

Conclusion

This study shows that it is possible for honeybees to both learn to discriminate between similar human faces and to subsequently recognise a target face when it is presented in conjunction with novel distractor faces. The findings indicate that it is possible for the visual and neural system of an animal to learn to reliably recognise a human face, even though the animal has no evolutionary history for the task.

We are grateful for technical assistance from Dr J. Schramme and Ms C. Schröder. A.G.D. is grateful to the Alexander von Humboldt Foundation for support.

References

- Bartlett, J. C. and Searcy, J. (1993). Inversion and configuration of faces. *Cognit. Psychol.* **19**, 473-497.
- Bruce, V. (1988). *Recognising Faces*. London: Lawrence Erlbaum Associates.
- Campbell, R., Pascalis, O., Coleman, M., Wallace, S. B. and Benson, P. J. (1997). Are faces of different species perceived categorically by human observers? *Proc. R. Soc. Lond. B* **264**, 1429-1434.
- Carey, S. and Diamond, R. (1977). From piecemeal to configurational representation of faces. *Science* **195**, 312-314.
- Chittka, L., Dyer, A. G., Bock, F. and Dornhaus, A. (2003). Bees trade off foraging speed for accuracy. *Nature* **424**, 388.
- Collishaw, S. M. and Hole, G. J. (2000). Featural and configural processes in the recognition of faces of different familiarity. *Perception* **29**, 893-909.
- De Renzi, E. and di Pellegrino, G. (1998). Prosopagnosia and alexia without object agnosia. *Cortex* **34**, 403-415.
- Duchaine, B. C., Dingle, K., Butterworth, E. and Nakayama, K. (2004). Normal greeble learning in a case of development prosopagnosia. *Neuron* **43**, 469-473.
- Dyer, A. G. and Chittka, L. (2004). Fine colour discrimination requires differential conditioning in bumblebees. *Naturwissenschaften* **91**, 224-227.
- Efler, D. and Ronacher, B. (2000). Evidence against retinotopic-template matching in honeybees pattern recognition. *Vision Res.* **40**, 3391-3403.
- Gauthier, I., Skudlarski, P., Gore, J. C. and Anderson, A. W. (2000). Expertise for cars and birds recruits brain areas involved in face recognition. *Nat. Neurosci.* **3**, 191-197.
- Giger, A. D. and Srinivasan, M. (1995). Pattern recognition in honeybees: eidetic imagery and orientation discrimination. *J. Comp. Physiol. A* **176**, 791-795.
- Giurfa, M., Hammer, M., Stach, S., Stollhoff, N., Muller-Deisig, N. and Mizrycki, C. (1999). Pattern learning by honeybees: conditioning procedure and recognition strategy. *Anim. Behav.* **57**, 315-324.
- Giurfa, M., Schubert, M., Reisenman, C., Gerber, B. and 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.
- Gould, J. L. (1985). How bees remember flower shapes. *Science* **227**, 1492-1494.
- Gould, J. L. (1986). Pattern learning by honeybees. *Anim. Behav.* **34**, 990-997.
- Henderson, J. M., Williams, C. C. and Falk, R. J. (2005). Eye movements are functional during face learning. *Mem. Cog.* **33**, 98-106.
- Horridge, G. A. (1996). Pattern vision of the honeybee (*Apis mellifera*): the significance of the angle subtended by the target. *J. Insect Physiol.* **42**, 693-703.
- Kanwisher, N. (2000). Domain specificity in face recognition. *Nat. Neurosci.* **3**, 759-763.
- Kanwisher, N., McDermott, J. and Chun, M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for the perception of faces. *J. Neurosci.* **17**, 4302-4311.
- Kendrick, K. M., Costa, A. P., Leigh, A. E., Hinton, M. R. and Peirce, J. W. (2001). Sheep don't forget a face. *Nature* **414**, 165-166.
- Lehrer, M. (1993). Why do bees turn back and look. *J. Comp. Physiol. A* **172**, 544-563.
- Lehrer, M. (1997). Honeybee's use of spatial parameters for flower discrimination. *Israel J. Plant Sci.* **45**, 157-167.
- Maddox, W. T. and Bohil, C. J. (2004). Probability matching, accuracy maximization, and a test of the optimal classifier's independence assumption in perceptual categorization. *Percept. Psychophys.* **66**, 104-118.
- Moscovitch, M., Winocur, G. and Behrmann, M. (1997). What is special about face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. *J. Cognit. Neurosci.* **9**, 555-604.
- Pascalis, O., de Haan, M. and Nelson, C. A. (2002). Is face processing species-specific during the first year of life? *Science* **296**, 1321-1323.
- Pierce, K., Müller, R. A., Ambrose, J., Allen, G. and Courchesne, E. (2001). Face processing occurs outside the fusiform 'face area' in autism: evidence from functional MRI. *Brain* **124**, 2059-2073.
- Rizzo, M. R., Hurtig, R. and Damasio, A. R. (1987). The role of scanpaths in facial recognition and learning. *Ann. Neurol.* **22**, 41-45.
- Srinivasan, M. V. (1994). Pattern recognition in the honeybee: recent progress. *J. Insect Physiol.* **40**, 183-194.
- Stach, S., Bernard, J. and Giurfa, M. (2004). Local-feature assembling in visual pattern recognition and generalization in honeybees. *Nature* **429**, 758-761.
- Standing, L., Conezio, J. and Haber, R. (1970). Perception and

- memory for single trial learning of 2560 visual stimuli. *Psychon. Sci.* **19**, 73-74.
- Tanaka, J. W. and Farah, M. J.** (1993). Parts and wholes in face recognition. *Quart. J. Exp. Psychol.* **46**, 225-245.
- Tanaka, J. W. and Sengco, J. A.** (1997). Features and their configuration in face recognition. *Mem. Cognit.* **25**, 583-592.
- Tarr, M. J. and Gauthier, I.** (2000). FFA: a flexible fusiform area for subordinate-level visual processing automated by expertise. *Nat. Neurosci.* **3**, 764-769.
- Tarr, M. J. and Cheng, Yi. D.** (2003). Learning to see faces and objects. *Trends Cogn. Sci.* **7**, 23-30.
- Tibbetts, E. A.** (2002). Visual signals of individual identity in the wasp *Polistes fuscatus*. *Proc. R. Soc. Lond. B* **269**, 1423-1428.
- Tibbetts, E. A. and Dale, J.** (2004). A socially enforced signal of quality in a paper wasp. *Nature* **432**, 218-222.
- Tranel, D. and Damasio, A. R.** (1985). Knowledge without awareness: an autonomic index of facial recognition by prosopagnosics. *Science* **228**, 1453-1454.
- Warrington, E. K.** (1996a). *Short Recognition Memory Test for Faces*. Windsor: Psychology Press.
- Warrington, E. K.** (1996b). *The Camden Memory Tests Manual*. Windsor: Psychology Press.
- Wehner, R.** (1981). Spatial vision in insects. In *Handbook of Sensory Physiology*, vol 7/6C (ed. A. Autrum), pp. 287-616. Berlin: Springer-Verlag.
- Yin, R. K.** (1969). Looking at upside down faces. *J. Exp. Psych.* **81**, 141-145.
- Zhang, S. W. and Srinivasan, M.** (2004). Exploration of cognitive capacity in honeybees: higher functions emerge from a small brain. In *Complex Worlds from Simpler Nervous Systems* (ed. F. R. Prete), pp. 41-74. Cambridge: MIT Press.