Through the Eyes of a Bee: Seeing the World as a Whole

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Abstract: *Honeybees are an important model species for understanding animal vision as free-flying individuals can be easily trained by researchers to collect nutrition from novel visual stimuli and thus learn visual tasks. A leading question in animal vision is whether it is possible to perceive all information within a scene, or if only elemental cues are perceived driven by the visual system and supporting neural mechanisms. In human vision we often process the global content of a scene, and prefer such information to local elemental features. Here we discuss recent evidence from studies on honeybees which demonstrate a preference for global information. We explore insights from imaging studies suggesting why a global preference may be important for foraging in natural environments where a holistic representation of elemental factors is advantageous. Thus we aim to provide a brief new insight into how animal vision may perceive the complex world in which we must all operate and suggest further ways to test this.*

Keywords: *Vision; local-global; Gestalt; Holistic; Flower; Wurmbea; Photography*

We often view and understand the environment around us in context (Torralba et al.), and humans are adept at visually perceiving a global construct or Gestalt of a complex scene (Sayim, Westheimer and Herzog). Although a review of these two concepts is beyond the scope of this work, here we employ the two terms interchangeably adhering to the terminology used by the authors of the cited papers. The Gestalt phenomenon is nicely illustrated in the famous finding of Navon (1977), aptly named 'Forest before trees: the precedence of global features in visual perception', which showed humans prefer the global construct compared to local elemental information within a scene. This work has been well replicated in several studies on human subjects, but surprisingly, most animals tested to date show a preference for local information (Navon 'The Forest Revisited: More on Global Precedence'; Deruelle and Fagot; Fagot and Tomonaga; Spinozzi, De Lillo and Truppa; Kelly and Cook).

Insect visual processing is somewhat complicated by the design of their eyes which consist of an array of many, thousands in some species, individual light sensing units (*omatidia*) packed in a small, compound eye (Land and Chittka). As a consequence of this design, insect vision has relatively poor resolution, 'image sharpness' compared to the larger human eye consisting on a single lens (Land and Nilsson).

In a well-studied insect species like the honeybee, it has typically been assumed that visual processing was relatively simple and mediated by elemental evaluation of cues (Horridge). However, for an animal with limited optical resolution, this may not be a very efficient solution as local elemental information available in a complex environment could easily be confounded with many other cues of similar appearance. This makes orientation and discrimination decisions difficult in complex environments (Adrian G. Dyer). For example, Figure 1 shows a photograph of a bunch of flowers imaged in the human visible spectrum and imaged through a mechano-optical device made of thousands of thin, black tube 'drinking straws' simulating the omatidia present in a honeybee's compound eye. This device allows us to obtain a visual representation closely simulating the resolution attainable by a honeybee's eye (Dyer and Williams) as measured through behavioural experiments (Srinivasan and Lehrer).

The upper panel in Figure 1 shows a magnified section of the image representing what an elemental processing type system might perceive in isolation, and how localised elemental information could be easily confused with different components within the entire image

(Figure 1, lower panel). This observation thus raises the question of whether honeybees indeed perceive a visually complex world by local elemental processing or if their visual system is capable of representing information more globally.

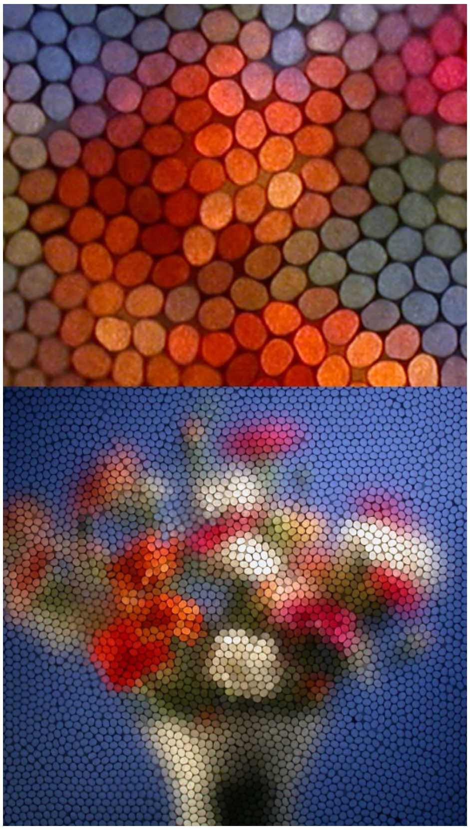

Figure 1. A human visible spectrum image of a bunch of flowers that have been captured through a mechano-optical device that closely matches the resolution of honeybee spatial vision (Dyer and Williams). The upper panel shows a segment of the image that would be easily confused with several parts of a scene, whilst the lower panel shows how a holistic view reveals the true shape and structure of the flowers. Whilst humans easily process the Gestalt of a scene, it was assumed insects like bees might only use elemental information. New work now shows that bees actually prefer global type processing, but can also pay attention to local elements within a complex scene (Aurore Avarguès-Weber, Adrian G Dyer, et al.).

The question of whether bees can perceive holistic information started to emerge as a strong possibility following a seminal publication by Stach et al. which showed that free-flying honeybees could indeed assemble local information to solve novel problems about the overall pattern of a more complex scene. Around this time, several studies also started testing the capacity of free-flying honeybees to learn very complex visual problems like different flower patterns (Stejskal et al.; Zhang et al.), landscapes (Dyer, Rosa and Reser; Zhang et al.), human artwork (Wu et al.) and even human faces (Dyer, Neumeyer and Chittka; Dyer and Vuong); whilst studies on other insect species like wasps also reported a strong capacity to recognise complex patterns like conspecific faces (Sheehan and Tibbetts; Tibbetts).

These studies on invertebrate vision were largely possible because of improved training and/or conditioning techniques employed by the researchers to train free-flying wild bees to visual tasks. Stimuli were presented vertically to control for orientation angle, and were learnt in relation to perceptually similar stimuli; termed differential conditioning (Giurfa et al.). Somewhat surprisingly, using these training techniques revealed a capacity in free-flying honeybees to process complex patterns including face-like stimuli, where bees showed evidence of configural type processing (A. Avarguès-Weber et al.). Indeed, prior to these studies configural processing was thought to be a mechanism requiring a large mammalian brain (Parr et al.; Tanaka and Sengco), and so it became high value to understand what else bees could learn to see if appropriate training regimes were employed. Despite having a miniature brain with less than one million neurons (compared to 100 billion in the human brain) (Srinivasan; Aurore Avarguès-Weber, Adrian G. Dyer, et al.), it has recently been shown that bees can learn rules such as the relative position of an object; above or below a given reference (Avarguès-Weber, Dyer and Giurfa), how relative size can allow for accurate recognition (Aurore Avarguès-Weber, Daniele d'Amaro, et al.), or even how multiple rules like above-below/left-right and same/different can be combined to solve novel visual problems (Aurore Avarguès-Weber, Adrian G. Dyer, et al.). The capacity to process information by applying rules such as above/below would enable faster and more reliable visual processing by bees when operating in complex environments (Chittka and Jensen), and strongly suggests that bees could simultaneously process more complex images than would be allowed by elemental processing (Adrian G. Dyer).

To test if bees could process complex scene information, it was possible to use hierarchical visual stimuli (Figure 2) as proposed by Navon (1977), which were presented to honeybees in a Y-maze to enable training and then testing with novel stimuli in which local and/or global information content was manipulated (Aurore Avarguès-Weber, Adrian G Dyer, et al.). In their experiment, free-flying honeybees were individually trained (using a sugar reward) to enter a Y-maze, which consists of an entrance hole, a long tunnel, and then a decision-making chamber which forks into two tunnels presenting two different options. The choice of a bee is counted once they choose which fork to fly down in order to hopefully receive a reward of sucrose (sugar water).

Somewhat surprisingly in the context of what is currently known about animal vision, bees learnt both local, the upright and inverted triangles in Figure 2, and global cues, the overall square or diamond shapes in Figure 2, from complex patterns during the training phase. Subsequently in the transfer tests where bees were presented with novel stimuli, bees preferred to rely on the global information to make decisions; but could also use local information if pre-trained to use the local elements to solve visual tasks. (Aurore Avarguès-Weber, Adrian G. Dyer, et al.).

This shows that a miniature brain can holistically process complex information and the reason why different animals may or may not share this capacity may be to do with environmental factors rather than brain size and complexity (Aurore Avarguès-Weber, Adrian G. Dyer et al.; Truppa et al.).

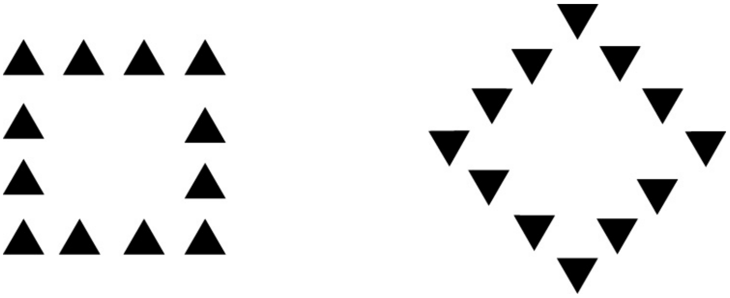

Figure 2. Visual stimuli used to test whether an animal will prefer to use global elements, the overall shape of each stimulus, or local information, the individual elements making up the overall shape, by (Aurore Avarguès-Weber, Adrian G. Dyer et al.) in their 2015 study.

This new evidence that bees can holistically process visual information leads to fascinating new questions about whether insect-pollinated flowers evolved certain shapes or morphologies to attract bee pollinators in a similar process to flower pigment colour, which has evolved to suit specific pollinator vision (Chittka and Menzel; Dyer et al.).

Honeybees demonstrate a preference for specific geometric traits such as radiating elements and symmetrical patterns (Lehrer et al.). In flowers, honeybees also prefer symmetry to asymmetry and radial symmetry over bilateral symmetry (Wignall et al.). To date, it has been questioned as to whether insects have the required optical resolution to perceive fine-scale differences across various levels of symmetry (Wignall et al.). With the aid of the mechano-optical device, we can now obtain insight into the level of symmetry fluctuations that a honeybee may be able to detect. The degree to which honeybees may perceive other morphological differences in flowers could also be examined using a mechano-optical device.

Interestingly, many insect-pollinated flowers have nectar guides or other striking patterns that would probably require the processing of multiple elements to perceive the overall pattern (Adrian G. Dyer; Guldberg and Atsatt). For example, Figure 3 shows a mechano-optical image of an Australian native flower, *Wurmbea dioica,* which has complex patterns that likely evolved for promoting visits by important pollinators such as native bees. *W. dioica* is a dioecious species, meaning plants are either male or female (Vaughton and Ramsey), presenting flower size dimorphism whereby male plants have larger and 'more showy' flowers than females (Barrett 'The Evolution of Mating Strategies in Flowering Plants'; Barrett 'Understanding Plant Reproductive Diversity'). Another sexual dimorphic trait of *W. dioica* is that male plants will have more flowers than females; both of these sexually dimorphic male characteristics result in attracting a higher number of bees (Vaughton and Ramsey). Using the mechano-optical device, we are now able to gain insight into how well a pollinator can differentiate between plants with more flowers and flowers of a larger size. We can examine this more closely by simulating different distances bees are at when making foraging choices, such as between sexual dimorphic individuals of *W. dioica*.

By developing new image processing techniques based on recent advances in digital imaging, it is now possible to dissect real floral patterns into their different spectral components, *i.e.* the colour channels in a digital image, in relation to their particular spatial configurations (Garcia, Girard, et al.; Garcia, Greentree, et al.). Indeed, the relationship between the different elements defining the spatial configuration of an object such as a flower, its variability within a species, and the visual background against which it is observed are the ultimate causes of visual perception by an animal (Troscianko et al.). However, data allowing for the understanding of these relationships from the point of view of an animal such as an insect pollinator are scarce. For example, a recent survey of Australian flowers using digital cameras calibrated for quantitatively assessing colour (Garcia, Greentree et al.), revealed a significant amount of within subject colour variability, which is very likely to be perceived by a pollinator. How then can an insect with relatively poor resolution cope with this variability and still recognise their target species in spite of slight changes in chromatic appearance? Or, can it be that the low resolution of the compound eye helps the insect by filtering out small variations thus facilitating object detection? The use of devices such as the mechano-optical device gives an insight into what a bee may see from a flower and helps us to answer these and other questions regarding the evolution of flower patterns in flowers.

By understanding how insect pollinators such as the honeybee see the world, it is also possible to improve current farming practices. For example, in agroecosystems using traditional farming techniques in developing countries, different plant species are planted along with economically important crops to reduce risk, manage pests and improve production (Altieri). In these contexts, knowledge of the visual appearance of insect pollinated plants from the point of view of a bee may assist on species selection in order to increase the saliency of target plant species, thus potentially improving pollination rate and therefore increasing harvest yield.

The design of optical devices simulating invertebrate vision such as the mechano-optical device described here creates new and exciting possibilities to better understand how animals see and interact with the world. In the case of bees, this information is of high value due to the contribution of these important pollinators to agriculture and food production.

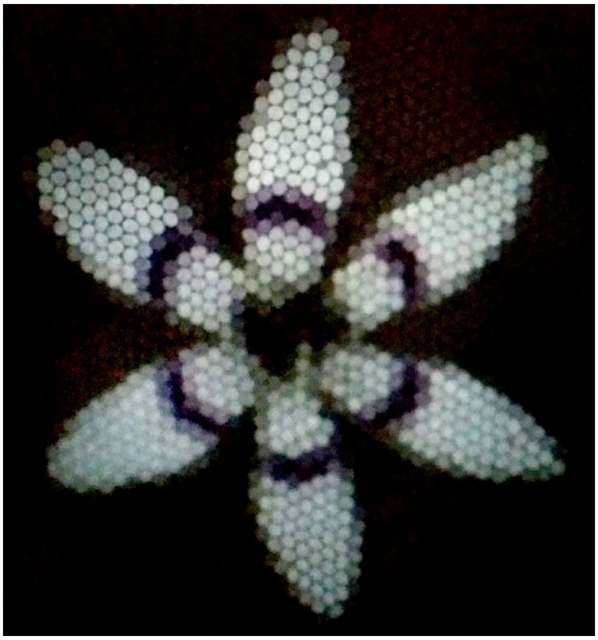

Figure 3. A bee's eye view of an Australian native *Wurmbea dioica* flower photographed through a mechano-optical device (Dyer and Williams 2005), showing the optics of an insect's compound eye can easily resolve details within a flower that may serve to improve recognition or orientation.

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