

The Craik-O'Brien-Cornsweet Illusion in Honeybees

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Humans perceive a low-contrast Craik-O'Brien-Cornsweet (COC) grating as being similar to, or even indistinguishable from, a squarewave grating (Fig. 1), despite the fact that the spatial intensity profiles of the two patterns are very different [3]. This similarity has been attributed to processing at early stages of the visual pathway which selectively transmits edge information, followed by cortical mechanisms which "fill in" the appropriate intensities between the edges [9]. Here we find that bees behave as though they experience a similar illusion, suggesting that certain principles of visual processing are shared by insects and humans.

While the visual systems of insects and humans display several differences – an obvious one being that insects possess compound (multi-faceted) eyes whilst humans possess simple (single lens) eyes – recent work is beginning to reveal several parallels with regard to the ways in which the two systems process visual information. For example, bees, like humans, possess trichromatic vision [16], are "colour-blind" with respect to the detection of motion [12, 13], appear to analyse pattern orientation by using orientation-tuned channels [20, 21] and even exhibit "top-down" processing with regard to the ability to detect camouflaged objects [22]. Indeed, insects even seem to experi-

ence some of the visual illusions that are experienced by humans. Flies, for example, behave as though they experience the Mueller-Lyer illusion [7] and the "waterfall" illusion [17], and bees behave as though they experience illusory contours [10, 11] and the Benham illusion [19]. These parallels could reflect the fact that humans and certain insects, despite carrying eyes that differ markedly in external appearance and optical design, may have evolved similar processing strategies because they must deal with similar visual environments and contingencies.

Here we continue the exploration of relationships between vision in insects and humans by investigating whether bees experience the COC illusion. The essence of such an illusion, shown in the center panel of Fig. 1, is that boundaries of surfaces influence brightness in such a way that the areas on opposite sides of the boundary are perceived as having different intensity even if their intensities are in reality identical. The reason for this illusion is that the intensity profile at the border (see the trace of the relative intensity in Fig. 1) suggests a transition from a light to a dark surface and is therefore interpreted as a signal for brightness change. Thus COC gratings are perceived by humans as being similar to squarewave gratings even if the two stimuli possess very different intensity profiles (see Fig. 1). Here we examine whether bees, like humans, perceive

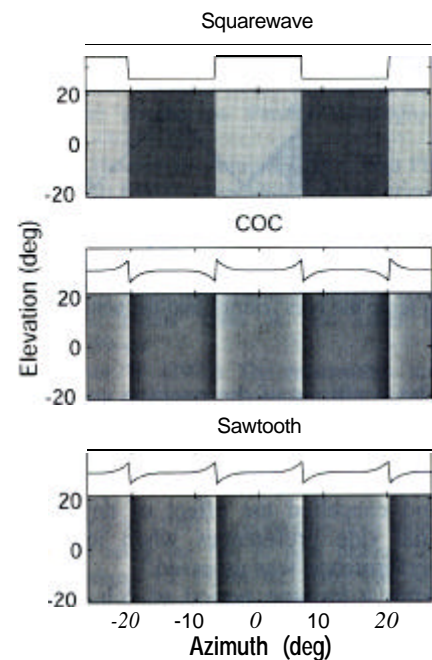


Fig. 1. Stimuli used in the investigation, shown together with their intensity profiles. Each stimulus was 26.5 cm wide and 20.5 cm high, subtending a visual angle 54° wide and 43° high at the decision boundary. Viewed from the decision boundary, the squarewave and COC gratings had an average period of 28.6°, and the sawtooth gratings an average period of 14.3°. The spatial intensity profile $I(x)$ of the COC grating was given by
$$I(x) = 1 + m \left(\frac{\pi}{2}\right)^{-4} \cdot [(x \cdot \text{mod} \cdot \pi) - \left(\frac{\pi}{2}\right)]^4 \cdot \text{sgn}[\pi - (x \cdot \text{mod} \cdot 2\pi)]$$
 where x denotes spatial phase (radians), m is the Michelson contrast, and
$$\text{sgn}(\theta) = +1 \quad \theta > 0$$
$$= -1 \quad \theta \leq 0.$$

The sawtooth gratings were described by a similar function, except that every second edge was reversed in polarity

COC and squarewave gratings as being similar.

About 1.5 freely flying bees were marked for individual identification and trained to enter a Y-maze apparatus which presented two visual stimuli, one on the vertical end wall of each tunnel (Fig. 2). One stimulus (termed positive) offered a reward of sugar water placed in a box behind the wall, which the bees could reach through a tube. The other stimulus (termed negative) carried no reward.

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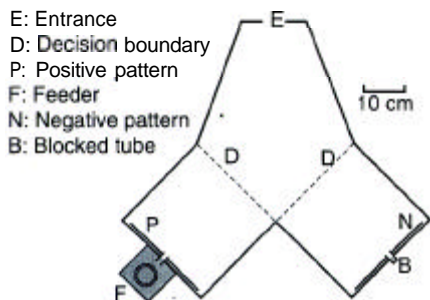


Fig. 2. The Y-Maze apparatus for investigating pattern discrimination. The dashed lines (D) are imaginary decision boundaries used to score the bees' entries into the tunnels

The positions of the positive and negative stimuli were interchanged every 10 min. This prevented the bees from developing a preference for one side, and cancelled the effect of any residual side preferences when learning performance was assessed.

After a training period of 6 h, corresponding to over 50 training visits per bee, the bees' discrimination performance was tested by measuring the choice frequency (CF) for the positive stimulus, i.e. the relative frequency with which the bees first chose the positive stimulus. Earlier studies using similar tasks found that the bees' learning curve attains a plateau after about 20 visits [10, 14]. A bee's choice was determined by noting which tunnel it entered first after arriving in the Y-maze, an entry being defined as a crossing of an imaginary plane (dotted line in Fig. 2). From the measured CF and the number of decisions counted (n), confidence levels (P) were generated using a one-tailed binomial test to determine whether the measured CF was significantly greater than the 50.0% level, corresponding to random choice. The reward continued to be present during the tests. In order to avoid possible effects of interaction between bees in the tests, a bee's decision was scored only if it was alone in the apparatus. Control experiments using identical stimuli in both tunnels indicated that the bees' choices were not affected by olfactory cues. Further details of training and testing procedures are published elsewhere [10]. A fresh group of bees was used for each training condition.

Three types of stimuli were used in the experiments: (a) COC gratings of contrast 0.5, (b) squarewave gratings of contrast 0.25, and (c) sawtooth gratings of contrast 0.5 (see Fig. 1). Between points of discontinuity, the profiles of the COC and sawtooth gratings were defined by quartic functions (details in Fig. 1 and [4, 5]). The stimuli were presented as photographs taken of an electronic display monitor (Barco CCID 7661). The monitor was driven by a display interface (AT Vista, TrueVision) controlled by an IBM-compatible (486) computer. Precise reproduction of the desired intensity profiles was achieved by gamma correction of the phosphor and the use of soft (linear) photographic film. In all experiments the bars of the gratings were oriented vertically unless specifically stated otherwise.

We first investigated whether bees can learn to distinguish between a squarewave grating and a COC grating. To humans these two stimuli appear very similar: each resembles a squarewave grating [9]. We found that bees could not be trained to discriminate between the two stimuli, displaying a frequency of CF for the positive stimulus which did not differ significantly from random choice. This was true regardless of whether the positive stimulus was the COC grating (CF=50.0%; $n=116$; $P=0.54$) or the squarewave grating (CF=52.9%; $n=153$; $P=0.26$).

Examination of Fig. 1 reveals that, to humans, the squarewave grating is more easily discriminable from a sawtooth grating than from a COC grating. We found that bees can be trained to distinguish between the squarewave and sawtooth gratings: the CF for the positive stimulus (sawtooth grating) was 61.9% ($n=126$, $P=0.003$). We also found that bees can learn to distinguish between the COC and sawtooth gratings: the CF for the positive stimulus (COC grating) was 63.3% ($n=128$, $P<0.001$). This task can also be learned if the sawtooth grating is made the positive stimulus during training: the CF for the positive stimulus (sawtooth grating) was then 65.2% ($n=253$, $P<0.001$). While these CFs are significantly different

from the 50% level, they are considerably lower than 100%. Perhaps this is not surprising, given that the discrimination tasks are rather subtle, at least to humans. Interestingly, the bees could not be trained to distinguish between two sawtooth gratings that are composed of edges of different polarity, despite being able to see both stimuli (see below): the CF for the positive grating was 51.0% ($n=263$, $P=0.40$).

In order to ensure that the bees could see and resolve all of the stimuli used in this study, we tested whether the bees can be trained to discriminate between horizontally and vertically oriented gratings of each type, in separate training experiments. The bees learned to make each discrimination very well (squarewave gratings: CF=81.0%, $n=153$, $P<0.001$; COC gratings: CF=82.2%, $n=141$, $P<0.001$; sawtooth gratings: CF=79.7%, $n=138$, $P<0.001$). All of these control experiments were carried out with the vertical orientation rewarded. However, earlier work on the discrimination of orthogonally oriented gratings [10, 21] indicates that discrimination is equally good regardless of which orientation is rewarded. Thus the bees were definitely able to see and resolve all of the stimuli that were used in the experiments.

One explanation for the similarity in appearance, as perceived by humans, of the squarewave grating and the COC grating is that centre-surround antagonism in the retina suppresses the lower spatial frequency components of the squarewave grating [3]. It is the information at low spatial frequencies that differentiates the COC grating from the squarewave grating. Centre-surround processing suppresses this information, causing each stimulus to evoke the same retinal response. Although there is as yet no electrophysiological evidence for centre-surround antagonism in the bee, such processing has been observed at early stages of the visual pathway in the fly [6]. Another explanation for the origin of the illusion in humans is that the visual system detects COC gratings as well as squarewave gratings in terms of peaks in the local energy distributions of their intensity profiles [2]. Since these energy distri-

butions are similar for the two profiles, and the peaks in both distributions signal the same kind of feature (an edge), the two stimuli appear identical. Our experiments so far do not allow us to distinguish which of the above hypotheses is valid for the bee.

It is interesting that the bees are unable to discriminate between sawtooth gratings of opposite edge polarity, even though (a) the gratings are visible to them, and (b) the sawtooth gratings are discriminable from the COC grating. Thus the bees can discriminate a sawtooth grating from a similar grating with half of its edges reversed (the COC grating) but not from one with all of its edges reversed. It would seem that the **apposing** edges in the COC grating create a unique perceptual effect, namely, one in which higher levels of the visual pathway "fill in" the intensity information between edges that is removed by the processing that occurs at the early stages. The sawtooth gratings of both polarities are visible to the bees, but as the edges of any given sawtooth grating all have the same polarity, they do not give rise to filling-in. Consequently, each sawtooth grating would be perceived as a series of vertical lines. The apposing edges of the COC grating, on the other hand, would give rise to a filled-in percept of alternately bright and dark bars, making this stimulus readily **discriminable** from a sawtooth grating.

An alternative possibility is that the bee's visual system does not perform filling-in, but that the sawtooth and COC gratings are distinguished from each other on the basis of the differences in the relative strengths of the Fourier components in the two stimuli. The sawtooth gratings of opposite polarities, on the other hand, differ from each other only in the relative phases of their Fourier components, and would be indistinguishable from each other if the bee's visual system were insensitive to phase. In addition, the squarewave grating would be indistinguishable from the COC grating because the two stimuli give rise to spatial response profiles that are identical in later stages of the visual system.

Regardless of whether the bee's visual system perceptually 'fills in' the missing intensities between adjacent edges of the COC grating, our results indicate that bees, like humans, **find** it difficult to distinguish between COC and squarewave gratings. This finding is consistent with the notion that information on edges is selectively extracted in the early stages of insect vision, as in human vision [3, 15]. Signalling edges, and suppressing the response to regions of the image where the intensity is relatively uniform, could have several benefits for vision. Firstly, edges are important in delineating objects and **recognising** them [15]; secondly, transmission of information from the retina to the brain is less redundant and metabolically less expensive if the responses are restricted to signalling spatial changes in intensity [1]; finally, accentuating edges may make the visual system more resilient to intrinsic noise [18]. The usefulness of **pre-processing** of this kind, followed by filling-in, has been demonstrated in the enhancement of radar images [8].

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