sensitivity to second-order motion [16,17] extends to depth perception. These results show a fundamentally unique neural computation of stereoscopic distance.

Mantises have fascinated people through history, tiny assassins waiting in the leaves and dispatching victims with fast, efficient strikes, inspiring artwork, mythology, and poetry. They have continued to inspire entomologists [18], neurobiologists [19], and even engineers [20], with their intriguing behaviors. This new work demonstrates that these behaviors, even with their convergent similarities to those of other animals, come from very different neural computations.

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## Visual Perception: To Curve or Not to Curve

### Barton L. Anderson<sup>1</sup> and David C. Burr<sup>1,2</sup>

<sup>1</sup>School of Psychology, University of Sydney, Sydney, NSW 2006, Australia <sup>2</sup>Department of Neuroscience, University of Florence, Via S. Salvi 12, Florence 56125, Italy Correspondence: barton.anderson@sydney.edu.au (B.L.A.), dave@in.cnr.it (D.C.B.) https://doi.org/10.1016/j.cub.2018.01.037

A popular new illusion shows that the apparent curvature of sinusoidal contours depends on contrast and background luminance. We suggest that the illusion is driven by segmentation mechanisms of human vision, which isolate the contours into smaller segments, some which approximate straight lines, others curves.

Everyone loves a good illusion and new ones continue to be discovered. Recently, Kohske Takahashi [1] from Chukyo University has described what he terms the 'curvature blindness illusion' (Figure 1A), which quickly drew the attention of scientists and social media. It is simplicity itself: a sinusoidal line is divided into two coloured segments, which alternate twice in each period. In one variant, the alternations occur at the peaks and troughs; in the other at the inflection points. Takahashi [1] reports that, on a white or black background, the two variants of the curves appear as they are, simple sinusoidal curves; but when the background is grey, the two sets of lines look completely different. One waveform appears as a smooth sinusoid, whereas the other now appears much more angular, more like a 'triangle wave': a series of linesegments changing orientation periodically. The illusion is dramatic, the sort you need to keep verifying to be sure that they are not playing tricks on you. And you cannot will it to go away. Why would the visual system make such a dramatic error in judgment, and why does it appear to be restricted to only some



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combinations of background and line colours?

Takahashi [1] suggests that the illusion is restricted to conditions where the polarity of the contour changes sign, and where the changes in the contour segments occur at the maximum and minimum of the sinewave. He bases his explanation on these assumptions, suggesting that the illusion arises from a competition between two sets of hypothesized detectors: obtuse 'corner detectors', which are present to detect discontinuous changes in orientation; and detectors specialized for detecting low curvature. He further assumes that 'corner detectors' respond to both the same and reverse polarity contour segments, whereas low curvature detectors only integrate segments of the same polarity.

Like many others, we were intrigued by the phenomenon, and sought to assess more thoroughly the empirical conditions that lead to the misperception of contour curvature. Our observations suggest that the illusion is not restricted to the conditions that Takahashi [1] reports, but is more general. Some examples are presented in Figure 1B where, like Takahashi [1], we present two pairs of contours on three different backgrounds. In the image at the top of Figure 1B, the background is mid-grey, and the contour segments change polarity; as Takahashi [1] originally reported, this leads to a strong illusion. But similar effects can be observed for luminance combinations on black and white backgrounds as well, where no polarity reversals occur. The illusory angularity of the pairs of contours on the black background (Figure 1B, middle) is only slightly weaker than that observed with the polarity reversed segments on the grey background. The illusion can also be observed on a white background (Figure 1B, bottom), although this appears to be the weakest variant of the three. Thus, although polarity reversals appear particularly effective in eliciting this illusion, they are not necessary, and appear only to modulate the strength of the effect. What, then, lies behind this dramatic illusion?

We believe that the abrupt contrast transition along the contours is a strong cue for image segregation, causing the light and dark contour segments to be





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#### Figure 1. The "curvature blindness" illusion.

(A) The original illusion presented by Takahashi [1]. Note that the pairs of contours on the intermediate background appear strikingly different, depending on whether a luminance change occurs at the inflection points or the max and min of the sinusoid. The line segments are the same two colours in all of the illusions. (B) Variants of the illusion in (A), but the line colours have been varied in the middle and bottom figures to enhance the segmentation of the contours into two segments. Note that the illusion is nearly as strong on the black background as the grey, and somewhat weaker on the white background.

treated as separate objects to be analysed in relative isolation. If true, the problem simplifies to understanding why the segmentation induced by a change in contour luminance at the peaks and troughs generates such a different percept of curvature from when the contour luminance changes at the inflection points. When the different segments of the contours are considered separately (Figure 2A), the illusion seems much less mysterious: the segments that span the maximum and minimum appear almost like a short line, whereas the other appears like an arc of a circle. Here few are surprised, given the physics of the situation: although both contain a half cycle of sinusoid (and therefore the same total unsigned curvature), the segment centred at the point of inflexion is well fit by a straight line, the other is not. This is self evident from a linear regression, obviously a good fit for segments demarcated by colour changes at the max and min.

The analysis presented above suggests that the illusion is driven by segmentation processes induced by the change in luminance of the contour segments. If true, any variation in strength of the illusion should scale with the strength of the segmentation processes that

decompose the contours into different segments. There are a number of different processes that could contribute to this segmentation process. One obvious segmentation cue is the contrast change across the different contour segments, which has both a sign and a magnitude. It is clear by visual inspection of Figure 1 that the perceived contrast difference of the segments is greatest with the grey background, which varies in both polarity and magnitude. The segments on the black and white background can only undergo a change in contrast magnitude. Contrast is generally defined as luminance differences (or range) normalized by some measure of the total luminance. Thus, contrast is higher on a black background than a white, which is consistent with our observations that the illusion is stronger on the black than the white background.

In addition to physical differences in contrast, there may also be other forms of integration that limit the amount of segmentation observed with contours that preserve polarity. The luminance relationships of the contour segments on the black and white backgrounds are consistent with the physics and perception of transparency [2,3], where the change in magnitude of contrast is

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decrements will effectively cancel; on the other hand, there will be a strong response for orientations orthogonal to the contour orientation, and hence a strong cue for segmentation. When only the magnitude of contrast changes, cells with both tangential and orthogonal orientations will be active, and mutually inhibit each other [6], generating a somewhat weaker segmentation cue. Thus, it may not be necessary to postulate a separate class of 'corner detectors' to account for the differences observed in these displays.

Perhaps the most important point made by this entertaining new illusion [1] is the fundamental role segregation plays in perception. Although the geometric patterns formed by the contour segments are identical, if the visual system is deceived into perceiving them as disjoint segments, we are compelled to see the two images differently. Each segment appears to be analysed on its own, without consideration of the neighbouring segment. And no effort of will can cause us to see the image in a different way, as a continuous curvy waveform. Unlike many other illusions, which exhibit perceptual bistability, this illusion is robust and unchangeable. This illusion like so many others - provides a striking window into the processes the visual brain uses to make sense of the world.

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#### Figure 2. Segmentation of the sinusoidal contours.

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(A) Upper figures: segments of the contours, separated either at the peaks of the waveform (top) or at the inflexion points. The lower curves show the best-fitting linear regression to the two segments, with the deviations from the fit shaded in grey. This region is 3.6 times as large for the bottom (curvy looking) figure as for the other. (B) Variants of Figure 1B, where the discontinuities are replaced by a continuous sinusoidal variation in luminance. This greatly reduces the segmentation of the contour into segments in all three images, particularly on the white and black backgrounds, which eliminates the illusion. The illusion is weakly present on the intermediate background, where some segmentation of the contour still occurs due to the polarity reversal.

attributed to a transparent layer overlying the lower contrast contour segments. Indeed, these luminance conditions induce a well known illusion, dubbed 'neon-colour' spreading [4]. It is difficult to determine the relative contributions of such 'mid-level' factors from low-level contrast explanations, as they are perfectly correlated in these displays. But if the segmentation explanation proposed here is correct, then the illusion should be reduced or eliminated if we reduce the strength of segmentation in these displays by eliminating the discontinuity in luminance. Figure 2B presents variants of the display where the intensity of the sinusoid varies smoothly (sinusoidally) with the contour. The illusion is reduced in all displays, but is almost completely eliminated in the displays on the black and white backgrounds, where both sets of contours appear identical in

shape. The contrast variations on the black background can appear as shadows or black smoke, whereas the lower contrast segments on the white can appear as being partially obscured by white fog. The illusion is still mildly present on the grey background, where the change in polarity still induces a segmentation similar to that presented in the original illusion.

What neural mechanisms could account for the different strength of segmentation in these displays? Most models of curvature perception exploit oriented linear filters similar to those observed in visual area V1 to account for the discrimination and perception of different curvatures [5]. For the stimuli where the contrast polarity reverses at the peaks and troughs, receptive fields oriented parallel to the line contours will be silent, as the increments and