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Seeing more than meets the eye: processing of illusory contours in animals

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Abstract This review article illustrates that mammals, birds and insects are able to perceive illusory contours. Illusory contours lack a physical counterpart, but monkeys, cats, owls and bees perceive them as if they were real borders. In all of these species, a neural correlate for such perceptual completion phenomena has been described. The robustness of neuronal responses and the abundance of cells argue that such neurons might indeed represent a neural correlate for illusory contour perception. The internal state of an animal subject (i.e., alert and behaving) seems to be an important factor when correlating neural activity with perceptual phenomena. The fact that the neural network necessary for illusory contour perception has been found in relatively early visual brain areas in all tested animals suggests that bottom-up processing is largely sufficient to explain such perceptual abilities. However, recent findings in monkeys indicate that feedback loops within the visual system may provide additional modulation. The detection of illusory contours by independently evolved visual systems argues that processing of edges in the absence of contrast gradients reflects fundamental visual constraints and not just an artifact of visual processing.

Keywords Perceptual completion · Subjective contours · Figure-ground segregation · Second-order contours · Single-unit responses

Introduction

Visual neuroscience ultimately strives to understand how brain mechanisms give rise to visual perception. To

that aim, we create stimuli whose physical attributes are characterized in great detail, measure if and how an animal subject perceives such a stimulus, and finally investigate neural responses in appropriate brain areas (ideally in the same, behaving subject) to generate computational algorithms. The brain, however, does more than just mirroring the outside world. It is involved in constructing perceptions that are formed on the basis of physical stimuli but go beyond provided sensory data. Such visual perceptions lacking a direct physical counterpart are often called visual illusions. Visual illusions provide a great opportunity to link perception and neural activity because they reflect the brain's active part in perceptual organization.

This article focuses on 'illusory contours', visual illusions that occur in contour perception. Contours in general provide important information about the shape of objects and are thus a key issue for the segregation of figures from the background. Detecting objects in a visual scene can be of vital interest. Potential prey subjects, for example, have to recognize their predator to be able to flee. Alternatively, prey can try to hide applying the strategy of camouflage, which is to minimize the number of visual cues that distinguish an object from its environment. (A chameleon, for example, is able to adopt color and texture of its environment, and even moves in a way that resembles a leaf moved by the wind.)

The predator, on the other hand, strives to 'break' camouflage by exploiting multiple visual cues and interpreting a visual scene. To detect object boundaries, luminance contrast is probably the most obvious cue. But the visual system gains precision in boundary localization when multiple cues (such as motion, texture, color or shading) are combined (Rivest and Cavanagh 1996). The ability to perceive illusory contours may, therefore, provide an 'anti-camouflage device' (Ramachandran 1987), evolved primarily to detect partly occluded or otherwise masked objects. This review article illustrates that (at least) species of insects, birds and mammals are able to see illusory contours, and

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that they are endowed with the appropriate neural network to perform such perceptual completion.

An outline of theories of vision and their views regarding visual illusions

‘Why do things look as they do?’ – the Gestalt psychologist Kurt Koffka (1935) circumscribed the central question of visual perception. This question has been answered differently over the years, but any consistent theory must provide an explanation for the occurrence of visual illusions. The following section tries to outline some core principles of important theories of visual perception and their point of views regarding visual illusions.

Gestaltism (Gestalt theory), introduced by Max Wertheimer, Wolfgang Köhler and Kurt Koffka, is a holistic theory of perception. They believed that perceptions had their own intrinsic properties as wholes (‘Gestalt’) that could not be reduced to the sum of their parts. Many configurations have emergent properties that are not shared by any of their local parts. This idea is strikingly illustrated by all sorts of visual illusions, and it is not an accident that the Kanizsa-triangle (Fig. 1) is named after one of the most important modern Gestalt psychologists (Kanizsa 1979).

James J. Gibson is the founder of the theory of *ecological optics* (Gibson 1979). He proposed that perception could be better understood by analyzing the structure of an organism’s environment, which he called its *ecology*. He believed in *direct perception*, the idea that visual perception is fully specified by the information available at the retina of a moving, actively exploring observer. Within the concept of *direct perception*, there was no space for visual illusions. Gibson claimed that illusions occur only under conditions that are ecologically invalid, that is, conditions that are seldom or absent in a natural environment. He insisted that ‘partial’ occlusions of surfaces (spatial dimension) are always ‘temporary’ occlusions (temporal dimension) in life (see Fig. 3). The animal that has ‘been around’

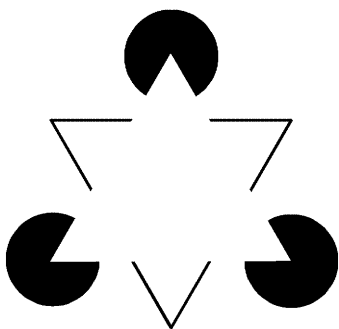


Fig. 1. The Kanizsa triangle is an example for modal completion. Illusory contours forming a triangle in the absence of corresponding luminance contrast changes. The interior of the triangle generally appears brighter than the ground, even though it is not

can ‘see’ things and places behind the modality sensed things and places, because ‘information’ and not ‘sensation’ is the basis of perception (Gibson 1966). Gibson’s theory profoundly inspired computational approaches to vision (Marr 1982) leading to the implementation of illusory contours in neural network models (e.g., Grossberg and Mingolla 1985; see later section).

Constructivism is committed to the idea that global percepts are constructed from local information. The original idea of constructivism goes back to Hermann von Helmholtz (1866), and was elaborated in modern times by Gregory (1972, 1980) and Rock (1983). Helmholtz proposed that perception depends on *unconscious inferences*. Unlike Gibson, Helmholtz acknowledged the logical gap between directly available sensory information and the perceptual knowledge derived from it (due to the so-called ‘inverse problem’ in visual perception; Palmer 1999). Helmholtz suggested that the gap could be bridged by using hidden ‘assumptions’ that are coupled with retinal information in an interpretation process to reach perceptual ‘conclusions’. Illusory contours are thought as assumptions to ‘explain’ surprising gaps in figures.

In this article, a constructivistic point of view in the broadest sense is adopted: Everything we see is a reconstruction based on information that is provided by interactions between matter and light. According to the wiring principles of the visual system, more or less ambiguous scenes are completed to construct a probable (or familiar) percept. Under most everyday circumstances, the matching of sensory data and the brain’s probability constructs are consistent with the actual states of affairs in the environment (a status called ‘veridical perception’). But if the underlying probability estimates (i.e., wiring schemes and neuronal algorithms) are false, the visual system is led to erroneous constructs, visual illusions.

Defining ‘visual illusion’

Defining ‘illusion’ is a notoriously difficult and often unsatisfying task. A common-knowledge answer might describe an illusion as something unreal, something that is actually not there. But it is unproductive to call all subjective attributes in perception ‘illusions’. ‘It seems better to limit ‘illusion’ to systematic visual and other sensed discrepancies from simple measurements with rulers, photometers, clocks and so on.’ (Gregory 1997). According to Gregory (1997), there are two distinct classes of illusions: those with a physical cause (optical disturbance intervening between an object and the retina) and knowledge-based, cognitive illusions. Examples for physically caused illusions are the refraction of light (erroneous perceptions of a bent stick when partly submerged in water) or the reflection of a mirror (we see ourselves *through* the looking-glass, yet we are in front of it). Cognitive illusions, on the other hand, are ‘due to

misapplied knowledge employed by the brain to interpret or read sensory signals' (Gregory 1997). Phenomena belonging to those 'cognitive illusions' are, for example, the Müller-Lyer illusion, the Ponzo-illusion or the Kanizsa-triangle (Kanizsa 1979). In the latter, we see a perceptually salient triangle formed by illusory contours (Fig. 1). Already described by Schumann (1990), the remarkable feature of illusory contours (also called *subjective, cognitive, anomalous, virtual or apparent contours*) is that they are seen as clear boundaries, although there are really no contrast or luminance gradients. (In a later chapter of this article, it will be discussed to what extent illusory contours can – or cannot – be seen as 'cognitive'.)

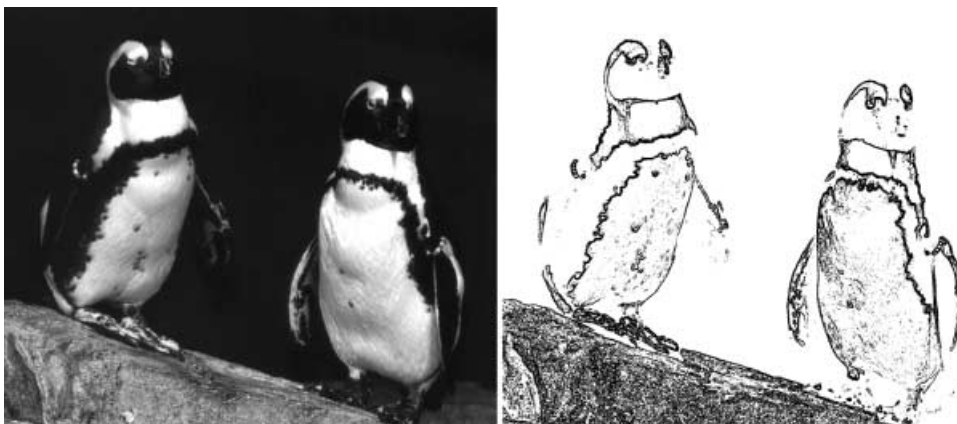
Illusory contour perception can also be regarded as a form (amongst others) of '*perceptual completion*' (Pessoa et al. 1998). Perceptual completion means that experimental subjects (animals or humans) report the percept of something in a particular visual region that is physically absent from that region, but present in the surrounding area. In other words, background elements induce a percept that has no physical counterpart at the very location it is seen.

Traditionally, perceptual completion has been subdivided into *modal* and *amodal* completion (Michotte et al. 1964). *Modal completion* refers to the perceptual completion of an object in the foreground of a scene, where all parts of the completed figure show the same attributes ('modes'). The famous Kanizsa triangle (Kanizsa 1979) is an example for modal completion (Fig. 1). Illusory contours are not only present in Kanizsa-type figures, but can also be generated by phase-shifting abutting gratings or gaps in background gratings that seem to occlude the background gratings (see Fig. 7A). Illusory contours are not extremely rare in

nature, but occur especially under low illumination quite often (such as in cluttered environments, during dawn or moonlit nights). As many raptors hunt during dusk and dawn (such as owls, for example), modal completion might indeed be of considerable advantage. Figure 2 illustrates illusory contours in a photograph of penguins.

Amodal completion, on the other hand, is the process of perceptually filling in parts of objects that are hidden from view; partly occluded objects (e.g., the circle in Fig. 3A) are perceived as completed behind other objects (as seen in Fig. 3B). Several findings support the idea that modal and amodal completion may indeed be related to each other and that illusory contours depend on the perception of occlusion. Line-induced illusory contours depend on the precise nature of the line termination (Kennedy 1988). The clearest perception of an illusory contour is achieved with abrupt line terminations (Fig. 4A), as when lines that are occluded by a closer edge terminate abruptly along the occluding contour. Occluded lines will not appear tapered to a point (Fig. 4B) or rounded at the end (Fig. 4C), and these conditions evoke no clear cut illusory contour. Kellman and colleagues (Kellman and Shipley 1991; Kellman et al. 1998) noticed that many illusory figures can take on an alternative appearance that produces amodal completion instead of illusory contours. The (slightly modified) Kanizsa triangle (Fig. 3E) can also be seen as a white triangle on a black background as viewed through three circular holes in an occluding white surface. In this case, the illusory contours are not seen, but the triangle is amodally completed behind the occluding white surface. Kellman et al. (1998) suggest that amodal and modal completion depend on a common underlying mechanism that connects edges across gaps. It seems that whether an observer perceives illusory contours or amodally completed contours depends on the perceived depth relations between the figures in question. If the missing contours are part of the closer occluding figure, then illusory contours are perceived. If the missing contours are part of the farther occluded figure, then they are amodally completed behind the closer figure (Palmer 1999).

Fig. 2A,B. Picture of two Black-Footed penguins (*Spheniscus demersus*) illustrating the occurrence of illusory contours in a natural scene. **A** We recognize the shape of the penguins in the photograph effortlessly. **B** The same photograph, but now only the luminance contrast edges (as detected by an image processing software) are shown. Although many borders of the penguins lack a contrast luminance gradient (note the incomplete edges at the heads, for example), they are perceptually (modally) completed in the original photography by the visual system



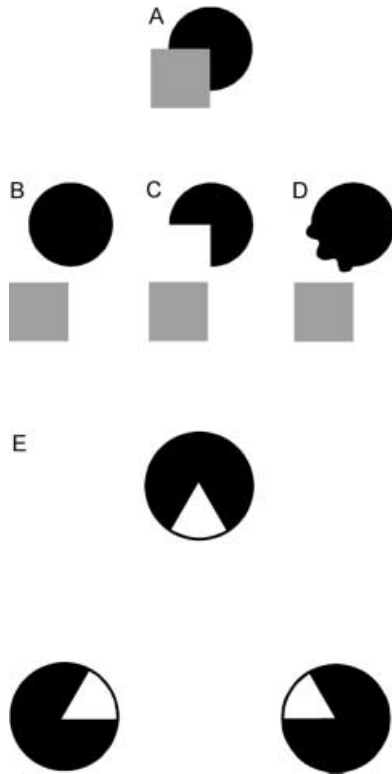


Fig. 3A–E. Amodal completion (occlusion). The partly occluded circle in **A** is perceived as completed behind the square (illustrated in **B**). It is not perceived, for example, as ‘pacman’ (**C**) or with variable outlines (**D**), although these completions would theoretically be possible. **E** A white triangle seen through black holes of a white occluding foreground

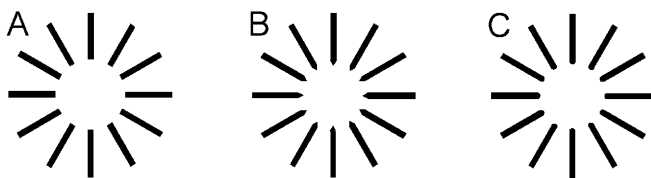


Fig. 4A–C. Influence of line terminations on illusory contour strength. Abrupt line terminations evoke strong illusory contours (**A**), while lines tapered to a point (**B**) or rounded at the end (**C**) do not produce clear cut edges

Perception and neuronal encoding of illusory contours in animal species

For a long time, the investigation of illusory contours was an exclusive domain of human psychophysics. This changed quite dramatically when von der Heydt et al. (1984) found that some single units in the visual cortex of fixating monkeys signal contrast borders and illusory contours. Their work became very influential in the following years and inspired behavioral and physiological investigations in several animal species. In support of a systematic approach that does not necessarily represent the historic development of the investigation of illusory contours in animals, the following paragraphs

are organized in a way that perceptual studies are described prior to neurophysiological recordings.

Mammals

Bravo et al. (1988) trained two cats in a two-choice discrimination procedure to detect an illusory square in one of two simultaneously presented displays. The illusory square was a Kanizsa-type figure generated by appropriately sectored disks (*‘pacmen’*) and was moving up and down in apparent motion. This illusory square was tested against a display composed of an array of sectored disks with the same overall configuration, but with the disks randomly rotated and, thus, not evoking an illusory square. The cats choose the correct display (by touching one of two response keys) in about 75–80% of the trials. Thus, the authors concluded that cats perceive shapes defined by illusory contours.

In a subsequent study, De Weerd et al. (1990) tested the ability of two cats to discriminate the orientation of illusory contours. The cats had to detect contours (real lines and illusory contours) with a reference orientation by pressing their noses against one of two nose keys through which the stimuli were viewed. Contours with an orientation that deviated from the reference orientation shown through the other nose key had to be ignored. Illusory contours were defined by gaps in circles and phase-shifted abutting semicircles (see Fig. 5, upper panels). The authors then measured the just noticeable difference (JND) in orientation, i.e., the difference in contour orientation (relative to the reference orientation) the cats were just able to detect. The cats could discriminate the orientation of real contrast contours most easily, resulting in smallest JNDs (around 5°, on average). But the animals were also able to discriminate the orientation of illusory contours with high precision. JNDs for the gaps-in-circles illusory contour was 11°, and 18° for the abutting semicircles illusory contour (Fig. 5). Furthermore, reducing the salience of illusory contours (through scrambling, density or line manipulations) resulted in increased JNDs in orientation. This confirmed that the cats used the orientation of illusory contours and not the position of some local cues to solve the task. Monkeys have also been trained successfully to discriminate the orientation of contours defined by illusory cues, amongst other contour cues (De Weerd et al. 1996). In studies on visual discrimination, Zimmermann (1962) showed that infant monkeys, which were trained to discriminate solid geometrical figures, showed an equally high performance for situations where only the outlines of the stimuli were present, or when parts of the outlines had been deleted, and thus, illusory contours emerged. The monkeys were able to discriminate the shapes without contours being physically complete.

In a pioneering study, von der Heydt et al. (1984) discovered single neurons in extrastriate visual cortex (V2) of the alert monkey that responded to illusory contours as well as to standard luminance contrast con-

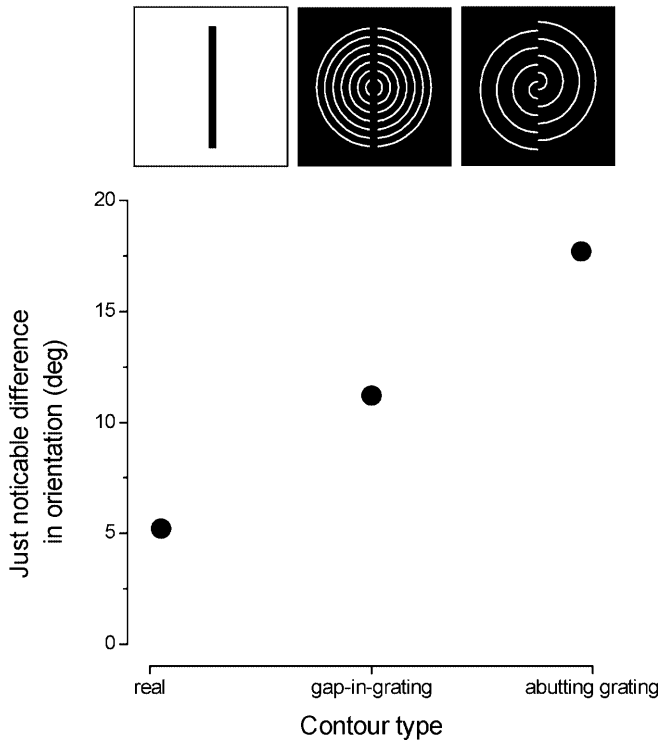


Fig. 5. Just noticeable difference (JND) in orientation of different contour stimuli for two cats. The scatter plot shows the average performance of both cats. Stimulus panels above the data points illustrate the contour stimulus. Data taken from De Weerd et al. (1990)

tours (Fig. 6). They found that 44% of V2 cells (and only 1 V1 cell out of 60) signaled the orientation of an illusory contour defined by abutting gratings (von der Heydt and Peterhans 1989). In an accompanying article, illusory contours were tested that appear in Kanizsa-type figures: a moving pair of notches in two bright rectangles mimicking an overlying, moving dark bar. Again, many V2 neurons (32%) responded to this kind of moving illusory bar, but only one V1 neuron responded out of 26 tested (Peterhans und von der Heydt 1989). Based on these results, the authors suggested that only V2 neurons are able to bridge gaps and to detect genuine illusory contours, whereas V1 responses specifically imply continuity of contrast borders (Peterhans and von der Heydt 1991).

This result – illusory contour coding in V2, but not in V1 – provoked a series of studies in both cat and monkey claiming some sort of responses to illusory contours in V1. These V1 responses to illusory contours, however, were interpreted in different ways, largely because orientation tuning to illusory contours was not determined precisely and V1 cells might have responded to the texture discontinuity without orientation tuning. The picture emerging from these studies is still puzzling. Redies et al. (1986) found neurons in feline V1 and V2 that signaled abutting grating illusory contours in addition to luminance contrast borders. This result was confirmed and extended by Sheth et al. (1996) using optical imaging and extracellular recordings in anaesthetized

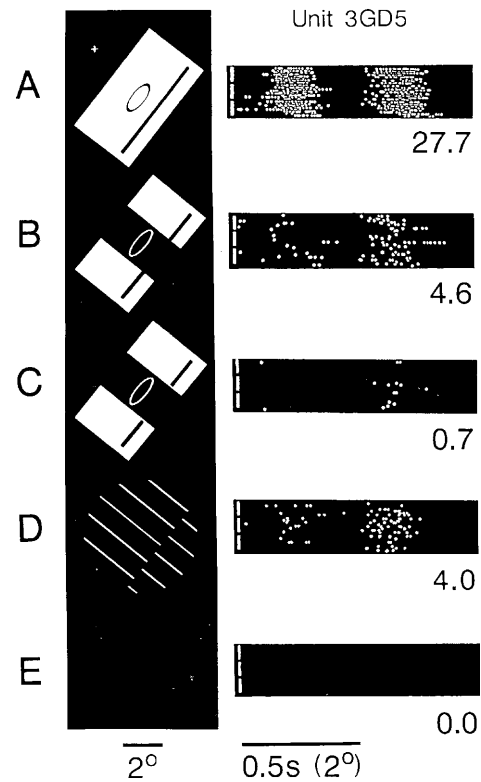


Fig. 6. Responses of a cell in V2 of an awake monkey. While the monkey is fixating the cross depicted in panel A, contours are swept back and forth across the neuron's receptive field (indicated by the ellipse). The right side of the figure shows the dot-raster displays that correspond to the stimulus images on the left. This cell responded nicely to a solid bar (panel A), as well as to an illusory contour defined by abutting gratings (panel D). Interestingly, the neuron also signaled a contour that seemingly bridges a gap (panel B), but discharge vanished when lines were closed (panel C) so that the illusory bar disappeared. (panel E) No stimulus presented. Numbers below each dot-raster display show average spike rate per cycle. From Peterhans and von der Heydt (1991). Reproduced by permission of Elsevier Science

cats. According to this study, 42% of V1 neurons and 60% of V2 units conveyed information about orientation of illusory contours defined by abutting gratings. In the anesthetized monkey, Grosz et al. (1993) reported the existence of V1 neurons that responded to both illusory and luminance contrast contours. The stimuli they applied (like phase-shifted abutting sine-wave luminance gratings), however, contained considerable local contrast borders and may not be regarded as 'illusory contours' according to the definition (see also Peterhans 1997; Ramsden et al. 2001; Lee and Nguyen 2001).

Two monkey studies represent the most recent contribution to the debate concerning the roles of V1 and V2 neurons in signaling illusory contours. Lee and Nguyen (2001) used a technique designed to call the monkeys' attention to a static display of a Kanizsa-type square while recording from visual cortex. In addition to the well-described V2 neuron responses, they also found significant responses of V1 neurons to illusory edges. Interestingly, illusory contour responses in V2 had a

shorter response latency compared to V1. Lee and Nguyen (2001) thus concluded that ‘contour completion in V1 might arise under the feedback modulation from V2.’ In anaesthetized monkeys, Ramsden et al. (2001) also found V1 responses to illusory contours in an optical imaging and single-unit study, but one that was quite different from V2 responses. Illusory contours evoked an ‘activation reversal’ relative to real contour activation in V1. V1 cells were suppressed by illusory contours (abutting gratings) presented at their preferred orientation determined with real contours, or even excited when illusory contours were presented orthogonal to their preferred orientation. Surprisingly, illusory contour processing led to a co-activation of orthogonal (inverted) orientation domains in V1 and V2. The authors concluded that such a mechanism ‘may be an important signal of contour identity and may, together with the illusory signal from V2, provide a unique signature for illusory contour representation’ (Ramsden et al. 2001).

Neurons responding to illusory contours are thought to have nonlinear properties, because in the Fourier spectrum of an abutting grating stimulus there is no energy corresponding to the precise orientation of the illusory contour. Based on computer simulations, however, Skottun (1994) pointed out that drifting abutting gratings in particular are able to stimulate neurons through the spatio-temporal properties of standard, linear receptive fields. While this is a serious criticism (Ohzawa 1999), the discrepancies between simulated and real neuronal responses indicate that linear filtering cannot account for all the response properties found in real neurons. For example, the neurons’ preferred orientation for drifting and stationary abutting gratings should be quite different according to the simulations, but the tuning of real neurons in the two conditions was usually similar (von der Heydt and Peterhans 1989). Moreover, linear filtering cannot account for responses to Kanizsa-type illusory contours when contours bridge gaps, but results for abutting grating illusory contours and Kanizsa-type illusory contours are in good agreement (von der Heydt et al. 1984; Peterhans and von der Heydt 1989; Lee and Nguyen 2001).

Birds

In a combined behavioral-electrophysiological study, Nieder and Wagner (1999) investigated the barn owl’s ability to see and encode illusory contours. Two owls were perched in front of a computer monitor and were trained to peck at a key to indicate whether they perceived a white-outlined square or triangle presented on a black background with thin, white parallel lines (Fig. 7A, left panels). Once the owls distinguished these geometric shapes with real contrast borders reliably, the contrast outlines of the figures were removed in transfer tests (that were occasionally inserted among ongoing baseline discrimination). In these transfer tests, illusory figures were first defined by small gaps in the back-

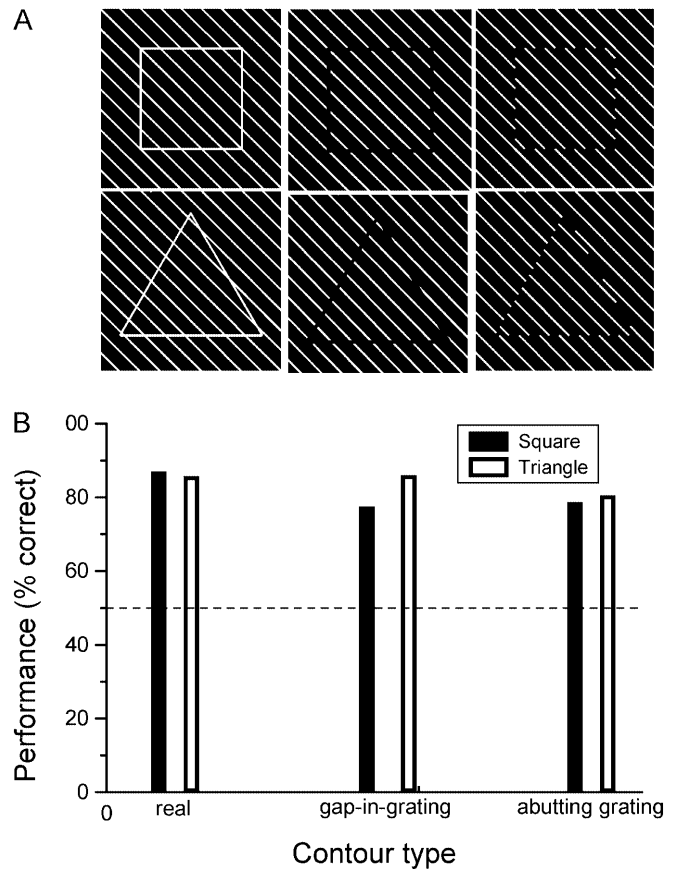


Fig. 7A,B. Behavioral testing of two owls to real and illusory contours. **A** Barn owls were trained to discriminate a white outlined square and triangle (*left images*). After the birds managed this task, illusory figures defined by gaps in gratings (*middle images*) or abutting gratings (*right images*) were occasionally displayed in transfer tests. **B** The owls reliably discriminated the two geometric figures, even when they were defined by illusory contours (after Nieder and Wagner 1999)

ground gratings (Fig. 7A, middle panels) or offsetting the parallel background lines (abutting gratings, Fig. 7A, right panels). As shown in Fig. 7B, both owls continued to distinguish the geometric shapes even when they were defined only by illusory contours. This suggests that the owl’s visual system interprets illusory contours as real borders. Illusory contour perception has also been demonstrated in chicks (Zanforlin 1981).

In neurophysiological investigations with two awake, fixating birds, Nieder and Wagner (1999) recorded single-unit activity from the visual Wulst (primary visual forebrain) via a small radio-transmitter attached to the birds’ head (Nieder 2000). The activity of neurons that responded well to moving bars was compared to illusory-contour stimuli (Fig. 8). All of the tested units responded to contours defined by gaps in gratings, and almost all of the contour-sensitive cells increased their activity significantly above baseline to illusory contours defined by 180° and 90° phase-shifted abutting gratings. To ensure that the neurons were sensitive to the global contour rather than to local image attribute (of the

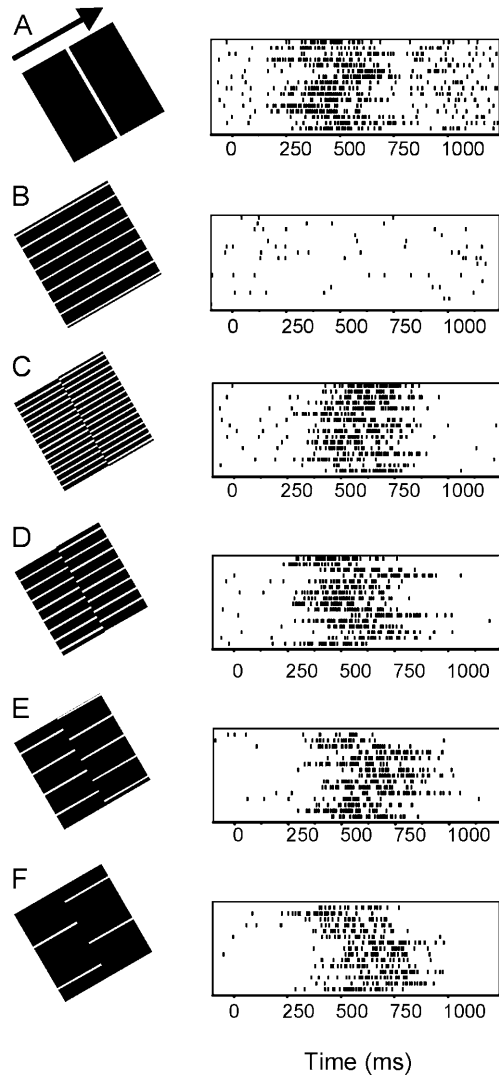


Fig. 8. Responses of a visual Wulst neuron to different types of contours. Real (panel A) and illusory contours (panels C–F) were swept across the receptive field in the direction indicated by the arrow in panel A. Dot displays on the right side of the figure show the time-course of discharge for several stimulus repetitions (each black dot represents an action potential). Stimulus panels on the left side show the contour type. The cell responded vigorously to a solid bar moved across the receptive field (panel A), as well as to abutting grating contours with line spacing of 0.25° (panel C), 0.5° (panel D), 1° (panel E), and 2° of visual angle. A grating with a phase shift of 0° for the background line (which, thus, showed no illusory contour) served as a control stimulus (panel B); the cell did not respond to the control (after Nieder and Wagner 1999)

grating lines, for example), the line spacing of the abutting grating stimuli was changed. Indeed, there was no significant difference between discharges to the four applied grating spacing of 0.25°, 0.5°, 1°, and 2° (Fig. 8, panels C–F).

Insects

Honeybees discriminate the inclination of edges in Kanizsa-type rectangles (van Hateren et al. 1990). Bees

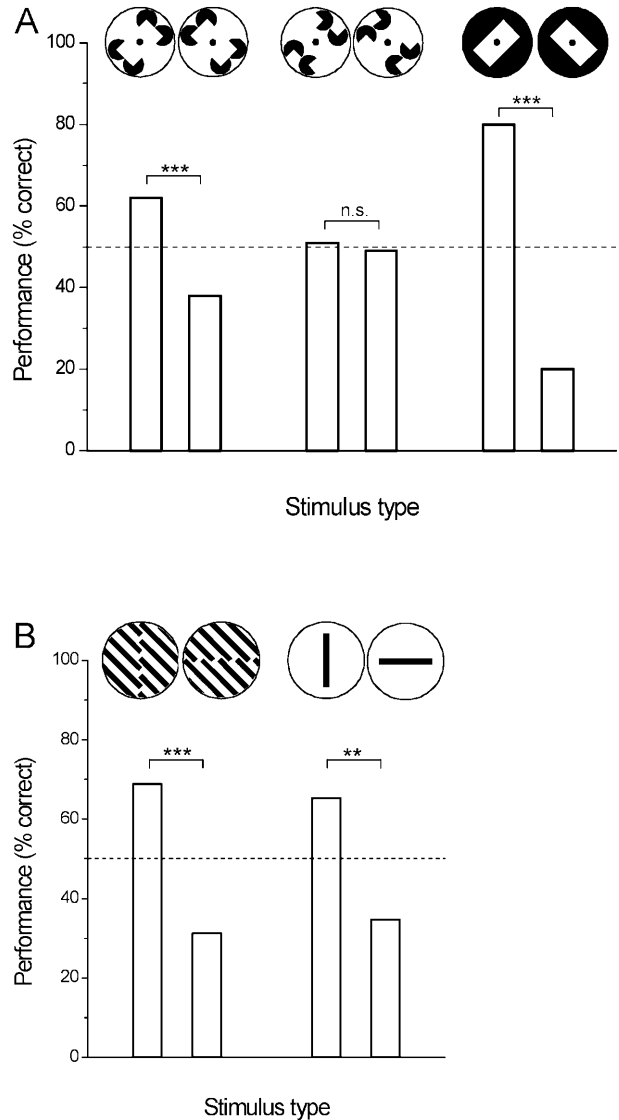


Fig. 9A,B. Bees perceive illusory contours. **A** Bees trained to choose striped patterns upwards to the right (positive stimulus) over striped patterns upwards to the left (negative stimulus) were able to discriminate the illusory (Kanizsa) rectangle with the appropriate inclination (left column pair) as well as solid rectangles (right column pair). They failed, however, when the illusion was spoiled by rotating the contour-inducing discs (middle column pair). Panels above each column illustrate the stimulus (***) $P < 0.001$, ** $P < 0.01$). After van Hateren et al. (1990). **B** Bees were trained to discriminate striped patterns containing a vertical (positive stimulus) and horizontal (negative stimulus) illusory contour. In subsequent tests, they significantly discriminated such patterns (left column pair) and solid single bars with the appropriate inclination (right column pair). After Horridge et al. (1992)

were trained to discriminate between regular striped patterns that were tilted upward to the right or downward to the right by choosing the correct route in a Y-shaped tunnel to get a reward – a sugar solution. After the bees managed this task, they were also able to discriminate solid rectangles as well as illusory rectangles with the appropriate inclination (Fig. 9A). As expected, bees failed in this task when the background dots

(‘pacmen’) inducing an illusory triangle were rotated and, hence, the illusion was destroyed.

Horridge et al. (1992) extended these results by testing honeybees in a behavioral protocol to discriminate horizontal or vertical illusory contours generated by abutting gratings. In a first set of experiments, the bees were unable to transfer the orientation of vertical and horizontal contrast stripes on which they were trained to matching orientations of illusory contours. However, when the insects were first trained to discriminate between patterns containing a horizontal or vertical illusory contour, they chose the corresponding orientation of solid bars and striped patterns in subsequent discrimination tests significantly more often (Fig. 9B). Horridge et al. (1992) also recorded (intracellularly) from a directional-selective, bar-sensitive neuron in the lobula of a dragonfly. This neuron responded strongly to a bar as well as to an illusory contour (again defined by phase-shifted abutting gratings) moved in the preferred direction. Both in the behavioral and the electrophysiological study, Horridge et al. (1992) used grating patterns with a spatial frequency of $0.16 \text{ cycles degree}^{-1}$ (1.5 cm bar width at a viewing distance of 27 cm), which is close to the honeybee’s visual acuity of $0.26 \text{ cycles degree}^{-1}$ (Srinivasan and Lehrer 1988).

Levels of explanation: bottom-up versus top-down processing

Traditionally, illusory contour perception has been explained by cognitive theories (Gregory 1972; Rock and Anson 1979). Illusory contour completion is seen as attempt to find the most likely solution to a perceptual problem. This view has changed quite dramatically in the past years. Surprisingly, some authors (Soriano et al. 1996) reject cognitive influences in illusory contour perception based on behavioral studies showing that animals (cats or insects) are obviously able to see subjective borders. But just because different species of animals perceive illusory contours, cognitive influences can not be ruled out. More important evidence favoring low-level explanations (or bottom-up processing) is provided by (1) electrophysiological recordings of single neurons, and (2) psychophysical studies in humans. The picture that emerges illustrates that bottom-up mechanisms are largely sufficient to explain a variety of perceptual completion phenomena, but feed-back loops might additionally contribute.

Electrophysiological recordings of single neurons

What was most surprising in the discovery of neurons that responded to both contrast and illusory contours was not the fact *that* such neurons exist (ultimately each and every perception will have a correlate in the nervous system), but *where* in the visual processing stream they are located. Cortical visual areas V1 and V2 are quite

early levels in the hierarchical processing of visual information. Neurons in these regions show restricted receptive fields and deal with quite basic tasks, such as contrast, binocular disparity, velocity and spectral component detection (for a review see Van Essen and DeYoe 1995). Higher up in the visual system, in inferior temporal cortex (IT), cells show more complex response properties suitable to cope with figure-ground segregation (Baylis and Diver 2001) and complex form recognition (Sheinberg and Logothetis 2001).

Similarly, responses to illusory contours were found already in the thalamo-recipient primary visual forebrain (visual Wulst) of owls (Nieder and Wagner 1999). The visual Wulst is the telencephalic recipient zone of the avian thalamofugal pathway in birds, which is the equivalent of the geniculostriatal pathway leading to visual cortex V1 and V2 in mammals (Karten et al. 1973). The physiological properties of the visual Wulst were found to mirror remarkably properties of the primary visual cortex of mammals as described by Hubel and Wiesel (1962). In the pigeon, Revzin (1969) found that neurons responded extremely well to moving images and exhibited small receptive visual fields that were retinotopically organized. Later on, Pettigrew and Konishi described a precise topographic organization, a high degree of binocular interaction, and selectivity for orientation, motion direction and binocular disparity in neurons of the barn owl’s visual Wulst (Pettigrew and Konishi 1976; Pettigrew 1979). Interestingly, the similarities between the primary visual forebrains of birds and mammals exist despite the fact that the binocular visual system in owls has evolved completely independently (Pettigrew 1986). And despite this independent evolution, illusory contours in both taxa (birds and mammals) are already processed a few synapses after the retina receives visual input.

Such early representation of illusory contours in strictly sensory brain regions argues for simple feed-forward mechanisms and against complex top-down influences from higher cognitive centers. Peterhans and von der Heydt (1991) proposed a network model to deal with contour coding: A ‘contour cell’ sums input from a (simple or complex) cell that detects contrast borders, as well as a set of ‘end-stopped’ cells with receptive fields oriented perpendicular to the contrast detector. ‘End-stopped’ cells respond best when a properly oriented line-end or corner is centered in the receptive field, but they are inhibited if an edge extends across its receptive field (Hubel and Wiesel 1968). Such end-stopped cells could signal systematic terminations of edges and lines that evoke illusory contours in abutting gratings or Kanizsa-type figures. This straightforward, feed-forward explanation, however, does not provide a full explanation of illusory contour phenomena. In particular, it can not explain why an illusory figure (like the Kanizsa figures) appears in front of the inducing elements, why the illusory triangle seems to be brighter than the background, and why some figures produce illusory contours while other, very similar ones do not.

Grossberg and co-workers (Grossberg and Mingolla 1985; Gove et al. 1995) provide a more complex computationally derived neural network theory that attempts to explain illusory contours and related phenomena (e.g., filled-in brightness). Instead of pure feed-forward connections (Peterhans and von der Heydt 1991), the neural network model in addition incorporates top-down feedback interactions (Gove et al. 1995). Cortical processing in the model is accomplished by two parallel but interacting streams (analogous to the mammalian blob and interblob stream). The first stream is primarily responsible for the generation of brightness percepts when lines group into closed illusory contours. The second stream generates boundary representations and illusory contours.

Also the most recent electrophysiological studies outlined above revealed more complex processing than pure feed-forward mechanisms. Lee and Nguyen (2001) found illusory contour responses in V1 cells that were delayed relative to V1 responses to contrast borders as well as to illusory contour responses in V2. Their data imply 'the involvement of lateral or feedback interactions in the contour completion process' (Lee and Nguyen 2001). The authors hypothesize that intracortical feedback of global contour information from V2 might enable a more precise representation of contours in V1 (as the neurons there show smaller receptive fields). Ramsden et al. (2001) draw a different picture based on their result in the anaesthetized monkey. The pattern of co-activation they found in V1 and V2 was correlated for real contrast contours, but out-of-phase for illusory contours. This pattern might resolve the ambiguity of whether a contour is a real contour or an illusory contour. In other words, V2 signals a contour, but the correlated or anti-correlated responses of V1 determine if the contour is 'real' or illusory, respectively. They further speculate that activation reversal in V1 cells during illusory contour presentation might be mediated through feedback loops from V2. This raises the question of how a V2 feedback loop could mediate both facilitation in one case (real contours) and suppression in the other case (illusory contours).

Psychophysical studies in humans

Several psychophysical studies suggest a common treatment of both illusory and contrast contours by the visual system. Particularly interesting in this context is the tilt aftereffect. When looking at lines oriented counter-clockwise from the vertical for a few seconds, a subsequently presented stimulus of vertical lines will appear tilted clockwise, away from the adapting orientation. Like contrast contours, illusory contours evoke a tilt aftereffect (Smith and Over 1975). Adaptation to real lines produces comparable tilt aftereffect with real and subjective test lines, but there is a significantly weaker tilt aftereffect when the adaptation stimulus is subjective and the test stimulus is real (Paradiso et al. 1989). Paradiso

et al. (1989) attribute the later finding to the physiological reports that only a subset of orientation selective cells in visual cortex is responsive to subjective contours. Taken together, there is a crossover between contrast and illusory contour tilt aftereffects, indicating similar sensory mechanisms (but see also Westheimer and Li 1997).

Can the neuronal responses account for the perception of illusory contours?

One of the fundamental problems neurophysiology is facing concerns the linking of perceptual phenomena with activity of single neurons. The vast majority of studies in this field rely on correlations between perception and neuronal activity, but correlations by no means establish causal relationships. We know that neurons that respond to illusory contours have been found in different animal species. How reliable is the assumption that neurophysiological responses of cells in the optic lobula of insects, the visual Wulst of birds, or V1/V2 of mammals represent the perception of illusory contour?

Robustness of single-unit responses to illusory contours

Humans have a vivid percept of illusory contours in abutting gratings even if the contour inducing background elements are varied. A similar independence from local features can be expected for neurons that should account for the global percept of an illusory contour. Humans rate the strength of illusory contours high for line spacings up to about 2° of visual angle (Soriano et al. 1996). Correspondingly, cells in V2 of the monkey as well as visual Wulst neurons in the owl respond vigorously to illusory contours for this range of line spacing (von der Heydt and Peterhans 1989; Nieder and Wagner 1999). Furthermore, the optimal range for single cell responses as a function of the number of lines in abutting gratings (7–13 lines) is in good agreement with human rating strength (von der Heydt and Peterhans 1989; Soriano et al. 1996). Finally, the perceptual rating strength is largest (i.e. illusory contour is most visible) for abutting gratings that are shifted by 180°, and declines more or less linearly when phase angle is reduced (Soriano et al. 1996). Mirroring this perceptual result, neurons in the owl's visual forebrain (Nieder and Wagner 1999) responded significantly less to illusory contour defined by a 90° phase shift (mean normalized response strength: 54%) compared to 180° phase shift (mean normalized response strength: 59%).

Abundance of single-unit responses to illusory contours

One would also assume that illusory contour coding cells should be abundant enough to account for a robust

percept. Unfortunately, only one cell is reported in insects (Horridge et al. 1992), suggesting that illusory contour neurons in insects might be quite rare. In the owl, however, Nieder and Wagner (1999) found that 91% of the tested cells responded significantly to subjective contours defined by phase-shifted abutting gratings. In the anaesthetized cat, 42% of V1 neurons and 60% of V2 units conveyed information about orientation of subjective contours defined by abutting gratings (Sheth et al. 1996), whereas 44% of V2 neurons in the alert monkey responded to these kinds of illusory contours (von der Heydt and Peterhans 1989). Taken together, neuronal responses in owls and mammals seem robust and abundant enough to represent a neural correlate of perceptual abilities.

Importance of the animal's internal state

When correlating neural activity with perceptual phenomena, the state of the (animal) subject during recording is an important issue. 'One often finds scientists making hypotheses about the physiological correlates of perception based on findings in animals that are not consciously perceiving anything due to anesthesia.' (Pessoa et al. 1998). How serious is this criticism? Physiologists would probably not argue that the response of a neuron, say to a pure tone in the auditory nerve, would change significantly whether the animal is awake or anaesthetized. Similarly, cells in the primary visual forebrain would signal a contour no matter if the subject is alert or under narcotics. The basic sensory processing principles in the brain have more or less been discovered under anesthesia. But anesthesia does definitely change neural responses, even in primarily sensory areas (e.g., Brugge and Merzenich 1973; Lamme et al. 1998; Schmidt and Konishi 1998; Capsius and Leppelsack 1998; Gaese and Ostwald 2001). And when it comes to linking perception and brain activity, the internal state of an animal subject might be of considerable importance. Whether an animal is attending to a visual stimulus or not, for example, has dramatic impact on a neuron's discharge (Moran and Desimone 1985; Treue and Maunsell 1996). Part of the discrepancy concerning illusory contour coding in V1 and V2 of mammals may be related to the mixture of awake and anaesthetized preparations in different studies. In general, results obtained from alert and behaviorally performing animals (von der Heydt et al. 1984; Nieder and Wagner 1999; Lee and Nguyen 2001) seem to be more reliable in terms of 'what is going on in the brain of a consciously perceiving animal'. Moreover, in the study by Lee and Nguyen (2001), the monkey had to attend to the location where the Kanizsa-square appeared, which might have contributed to the illusory contour response in V1. Similarly, another perceptual completion phenomenon called perceptual filling-in, which was present in V2 and V3 neurons of awake monkeys (De Weerd et al. 1995), was absent in anaesthetized monkeys (De Weerd 1998).

In summary, it would be desirable to have more neural data from animals that were trained to actually see illusory contours while recording. This would help to elucidate illusory contour processing in consciously perceiving animals and reduce different sources of artifacts.

Other second-order (non-Fourier) contours

This article concentrates on illusory contours (namely abutting gratings, gaps-in-gratings and Kanizsa-type figures) that have been used in many behavioral and electrophysiological studies. Because illusory contours are gradient-free, they have also been termed 'second-order' stimuli. Chubb and Sperling (1988, 1989) refer to first-order stimuli as Fourier stimuli and second-order stimuli as non-Fourier stimuli. This is because the energy of moving luminance stimuli may be well-described by the Fourier transform of the position of the luminance pattern over time. However, since second-order stimuli do not contain differences in luminance between stimulus and surround, there is no energy pattern from which to extract a Fourier transform. Luminance and color are called first-order cues because they are directly sensed by the visual system. Retinal disparity, relative motion and texture are termed second-order cues in that they are not detected directly, but derived. These cues are outlined in the following, but an in-depth treatment is beyond the scope of this paper.

Binocular horizontal disparity in random-dot stereograms (RDS; Julesz 1971) gives rise to sharp illusory contours at the depth-induced edges. Recently, von der Heydt et al. (2000) recorded from neurons in V1 and V2 of the alert monkey while presenting stereoscopically defined edges in RDS. Many cells in V1 and V2 responded to disparity of stereoscopic surfaces, but only cells in V2 (17% of the sample) were found that responded selectively to the orientation of stereoscopic (as well as contrast) figure edges. Of these cells, the majority even signaled the step polarity of the contour. Thus, 'figure/ground segregation and the elaboration of occluding contours are primary goals of processing in area V2' (von der Heydt et al. 2000). Unfortunately, it is not known whether visual Wulst cells in the barn owl would show similar properties. One might speculate, however, that some neurons in the owls Wulst would signal polarity and orientation of edges in RDS, because owls possess global stereopsis comparable to humans (van der Willigen et al. 1998) and neurons have been recorded in fixating owls that responded readily to disparity in RDS (Nieder and Wagner 2000, 2001). Maybe the 'obligate binocular neurons' that only responded when a bar with the appropriate disparity and orientation was swept across the receptive fields (Pettigrew 1979) would be good candidates for stereoscopic edge detectors.

The *motion* domain equivalents of RDS are kinematograms. In kinematograms, vivid boundaries are

produced when a centrally located set of random dots is moved coherently in one direction while the surrounding dots are moved in a different direction. 'Thus they constitute a pure motion stimulus because the form is only visible in the dynamic pattern, but not on any single frame' (Frost et al. 1990). Frost et al. (1988, 1990) explored how deep cells of the pigeon's optic tectum (superior colliculus in mammals) respond to kinematograms and edges in dynamic kinematograms. Tectal cells signal the edges of kinematograms. Even more, cells signaled whether the edge was an occluding or disoccluding boundary (Frost et al. 1990).

Leventhal et al. (1998) recorded responses of V1 and V2 neurons in the anesthetized monkeys and cats to isoluminant *texture*-induced boundaries. Texture-induced boundaries were generated by random-dot patterns, with a central 'bar' region defined by dots of larger size than the background. Few cells in V1, but many cells in V2 signaled orientation of such borders.

It remains to be tested to what extent such neurons responding to individual second-order cues are able to integrate contour information across a variety of visual parameters (like luminance, color, disparity, texture, motion, etc.). Maybe some of these cells would signal an object border no matter how it is defined, whether by a first-order cue or any second-order cue. Such neurons might possess the properties of abstract contour detectors.

Concluding remarks on the functional significance of illusory contours

It has been hypothesized that the ability to perceive illusory contours may provide a strategy to detect borders of camouflaged objects (Ramachandran 1987). Dresp and Spillmann (2001) suggest that illusory contours 'reflect the output of brain mechanisms that have evolved to fill in gaps in physically incomplete stimuli'. If that is true, we might expect that different animal species with divergent and independently evolved visual systems are able to perceive illusory contours. This review article illustrates that (at least) species of insects, birds and mammals are able to see illusory contours, and that they are endowed with the appropriate neural network to perform such perceptual completion. In the studied animal species, the detection of contours without luminance contrast gradients takes place at early levels of the visual system, largely independent from top-down influences. This finding supports the above hypothesis, because mechanisms that are relevant for an animal's survival (for example, in the prey-predator interaction) have to be fast, efficient, and foolproof (Dresp 1997; Dresp and Spillmann 2001).

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