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On «illusory» contours and their functional significance

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Abstract

Evidence from neurophysiology and from behavioral studies on non-human vertebrates and invertebrates suggests that the early processing of illusory contour information relies on adaptive visual mechanisms. The significance of such mechanisms for the survival of various species is about to become an increasingly important issue in our understanding of newly discovered phenomena of visual adaptation and perceptual learning. Neurophysiological and computational approaches together with a consistent body of evidence from visual psychophysics have helped to shed light on the mechanisms underlying contour integration, contour completion, virtual borders, and the perceptual emergence of illusory contours. This article reviews some of the major empirical evidence suggesting a common functional significance of real and illusory contours and then sets out to demonstrate how these functional aspects can be studied by finely tuned psychophysical techniques.

Key words: Illusory contours, filling-in, adaptive mechanisms, subthreshold summation

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> *"We can only know in the nervous system what we have known in behavior first"*
> (Julian Jaynes, 1990)

INTRODUCTION

Why do we see the world in terms of forms and objects that are delineated by neat, well-defined contours, and not just vaguely blurred boundaries? Why can we detect misalignments of contour fragments with an accuracy that transcends by as much as a factor of 10 the limits of acuity of the receptors in the visual system? How can we explain the extraordinary perceptual capability of man to see unambiguous shape contours in images that contain only a few scattered stimulus fragments? What is the nature and the function of the perceptual processes which generate clearly visible boundaries in stimulus configurations without receiving any local input in terms of a difference in physical luminance? The astonishing capacity of man to perceive visual alignment and form boundaries under seemingly difficult conditions must obviously rely on mechanisms which efficiently cope with situations where sensory input is partially inadequate or even lacking completely.

Earlier theories concerned with the perception of object contours under such conditions (e.g., Gregory, 1972; Rock, 1987; Parks, 1989) have emphasized the determining influence of cognitive processes, notably object identification, on the capability of the human perceptual system to extract contour information from a physically rather "unsatisfactory" stimulus support. Then, explaining the perception of contours and shape boundaries was conceptually not possible without reference to a cognition-dependent analysis of the visual world in terms of figure and ground, what belongs where, and the hiding and the hidden (see Spillmann & Dresp, 1995, for a review). Recent developments in the field of form vision, especially the discovery of "context sensitive" visual neurons in the monkey cortex (Peterhans & Von der Heydt, 1989; Von der Heydt & Peterhans, 1989; Gilbert & Wiesel, 1990; Das & Gilbert, 1995; Kapadia, Ito, Gilbert, & Westheimer, 1995), indicate that the classic approach to form perception in cognitive psychology finds itself confronted with new challenges. It appears that we now have to reconsider and to reanalyze some major issues regarding the visual perception of form and the growing body of neurophysiological and psychophysical evidence seems to call for a theoretical framework that takes into account specific environmental constraints and the idea of biological mechanisms having evolved as a response to these constraints.

The first part of this article is concerned with the review of some critical findings from animal behavior studies, including earlier experiments on contour and form vision in goldfish, octopus and other invertebrates, as well as more recent investigations in honeybees. The biological plausibility of a functional equivalence of "real" and "illusory" contours is discussed on the basis of examples of situations of environmental constraint like partial stimulus occlusion or biological camouflage.

The second part of the article deals with the visual psychophysics of contour completion, and the necessity of designing experiments which "simulate" some of the specific environmental constraints that influence the possibility to extract contour information from visual environments. A context analysis concerned with purely local stimulus factors such as alignment, spacing, length, and contrast polarity of visual fragments, is suggested. The extent to which these factors determine contour extraction at different levels of processing, including subthreshold detection, is discussed on the basis of "trendsetting" psychophysical data on contour integration by the visual system.

SPECULATIONS ABOUT THE BIOLOGICAL SIGNIFICANCE OF "REAL" AND "ILLUSORY" CONTOURS

Contour is presumably the most critical part of any form or object, and can be detected easily without the physical stimulus carrying the information having to be complete or perfectly visible. Some experimental studies suggest that the alignment or collinearity of stimulus fragments is sufficient for contour detection or edge extraction (Bonnet & Dresp, 1991) and it has furthermore been shown that the latter is a prerequisite for object recognition in cluttered visual scenes (e.g., Biederman, 1987).

Evidence for a functional equivalence of real and virtual, or illusory, contours comes from various studies showing that they all behave in the same way, engender the same perceptual consequences. This holds for tilt aftereffects and orientational masking (Smith & Over, 1975, 1976, 1977; Paradiso, Shimojo, & Nakayama, 1989), apparent motion (e.g., von Grünau, 1979; Ohmura, 1981; Mather, 1988), and kinetic and stereokinetic effects (Kellman & Cohen, 1984; Bruno & Gerbino, 1991). The McCollough orientation-contingent color aftereffect, usually observed with patterns of fully visible black and white stripes, has recently been found to be elicited in the same way by partially occluded but perceptually continued contours (Watanabe, 1995).

Making a clear distinction between the simple detection of contours and more complex performance such as their analysis, identification, or categorization is important. It is argued here that the first biological role of a visual system is to detect things in the environment (Ungerleider & Mishkin, 1982), before assigning a location (*where?*), an identity (*what?*), or a context. After detection, the assignment of an identity or a function of an object can be achieved by whatever means are available, and these are not necessarily mediated visually (Kulikowski, 1991). In fact, once the attention has been drawn to a visually detected object, all other senses and the whole cognitive machinery can be focussed on it. Object identity could then be conveyed by sound, smell, or touch much more efficiently than by looking at it longer, especially under circumstances of bad visibility, or at night. Moreover, the information that *something* is there may, under extreme circumstances, be far more relevant than knowing precisely *what* there is. The unexpected and sudden detection of a thing that cannot be immediately identified automatically gives rise to a significant reaction within the organism, alerts it, puts it into a condition that can be followed by immediate action if necessary. As a consequence, mechanisms of visual detection would certainly fulfill an important "warning function" within a biological theory of visual perception.

Considering the biological function of detection and the preparation of action as one of its behavioral consequences, the question whether shape contours could act as "visual releasers" has been raised. Among biologists, it is now a well-acknowledged fact that even some of the most routine-like, and previously considered as "innate" or "instinctive", behavior chains are modulated by learning and the necessity for adaptation to new ecological constraints. The trigger-stimuli for typical behavior patterns of animals exhibit a surprising complexity and variety, even if we consider species with relatively simple neural systems. A brief review of some earlier and some more recent behavioral studies with animals make the idea that contours of shapes, including illusory contours, may fulfill the role of something that ethologists or zoologists would call a "visual releaser" seem plausible

Contour as a visual releaser?

Specific behavior patterns of individuals of many species are largely determined by visual releasers or visual sign-stimuli. Apart from color, which is a well known visual releaser for sexual and parental behavior patterns in various species, there is evidence that shape contours play an important role for any behavior that necessitates the visual detection of objects in space. Examples would be navigation strategies or orientation in space in a broader sense, prey capture, as well as avoidance of imminent or potential dangers in a more specific context.

Although the amount of evidence is not abundant, the most fundamental behavioral observations here date back to the early work by Goldsmith (1914), Herter (1929, 1930, 1953), Perkins (1931), or Maes (1930), suggesting that minnows and goldfish discriminate shapes such as circles, squares, triangles, or crosses on the basis of contour when size and color do not vary. Sutherland (1960) made similar observations with the octopus and noticed that some contours defining specific shapes immediately and systematically triggered attack behavior. Wehrhahn and Reichhardt (e.g., 1973) found that the visual orientation in space and navigation strategies in houseflies are essentially guided by horizontally oriented contours. Evidence for contour as an important visual cue for the navigation behavior of honeybees comes from recent observations by Lehrer and Srinivasan (1993, 1994). Honeybees instinctively follow the contours of objects during flight (Lehrer & Srinivasan, 1993), and in laboratory tasks such as pattern discrimination they tend to fly along the most salient contours in the stimulus pattern. Interestingly, they can also learn to suppress the innate contour-following behavior when other flight strategies are required to cope with a new situation (Lehrer & Srinivasan, 1994).

The ability to detect virtual and illusory contours was found in animals with anatomically different visual systems including very young human primates. Some aspects of contour interpolation in non-human primates are illustrated by the results from the studies on visual discrimination in infant monkeys by Zimmermann (1962). Figure 1 shows stimuli the discrimination rates of which are equivalent for 11 days old rhesus monkeys. When trained to discriminate, for example, a solid black circle and a black square (only responses to the circle are rewarded, for instance), a close to 100% correct performance is obtained after the training period. Generalization tests revealed that the performance remains equivalent in situations where only the outlines of the stimuli are presented, or when parts of the outlines have been deleted and bright illusory patches emerge locally within the stimuli. Contour discrimination is thus generalized for shapes without a contrast or color surface, and without contours being physically complete, suggesting that the animals can recover the global shape of the stimulus on the basis of fragments. Interestingly, it has been shown that young human infants have that same perceptual ability to reconstruct global forms from contour fragments (Gollin, 1960; Abravanel, 1982). Preferential looking techniques have shown that this completion phenomenon is also observed with babies who are only three to seven months old (Bertenthal, Campos, & Haith, 1980; Ghim, 1990).

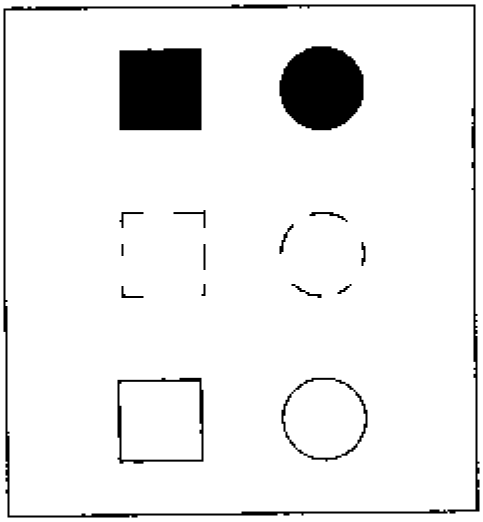

Figure 1. Visual forms of the type used in the experiments by Zimmermann (1962) on the generalization of shape discrimination in infant monkeys. The three form pairs (filled square and circle (a), outlined square and circle (c), outlined square and circle with partially deleted contours (b)) yield equivalent discrimination performance in young monkeys that have been trained to discriminate the filled square and circle.

Animals which do not have a visual cortex seem to be able to detect illusory or interpolated contours. This is illustrated in the fascinating work by Horridge, Zhang, and O'Carroll (1992) and Hateren, Srinivasan, and Wait (1990). By means of specifically designed test tubes and a sugar-versus-no-reward technique, Horridge et al. (1992) trained groups of "research-minded" (cit. page 59, second paragraph) bees to discriminate a pattern with vertical stripes from a pattern with horizontal stripes. After training, the bees were shown a vertical and a horizontal illusory contour, and discrimination performance was found to be equivalent. Note that no other cue for horizontal or vertical orientation was available in the illusory contour configurations. As already mentioned above, the ability to detect contour, or aligned contour fragments, has been found to be of some general importance for bees with regard to navigation strategies (e.g., Lehrer & Srinivasan, 1994). Hateren, Srinivasan, and Wait (1990) have found that flying bees can also detect illusory target contours induced by the collinear edges of a physical stimulus, like those that can be seen in Kanizsa squares. For human observers, these latter give rise to particularly strong sensations of interposition and partial occlusion. A relation between the bee's abilities to detect edge-induced illusory contours and the necessity to detect partly hidden objects during flight is therefore not unlikely. Beyond the behavioral data, Horridge et al. (1992) have found a neural correlate of illusory contour detection in insects, which are animals with relatively primitive visual systems compared to that of non-human primates or man. The authors recorded the firing behavior of a single, motion-sensitive neuron which is not selective to a particular orientation and which is located in the optic lobe of the dragonfly (*hemicordulia tau*). It was found that the cell starts firing when an illusory contour is shifted across its receptive field.

Apart from the evidence that insects can detect shapes with illusory contours, there are other data indicating that cats (Bravo, Blake, & Morrison, 1988; Corbetta, Antonini, Berlucchi, & Aglioti, 1989; De Weerd, Vandenbussche, De Bruyn, & Orban, 1990) and also chicks (Zanforlin, 1981) discriminate illusory contour stimuli in a similar way as they discriminate stimuli with real contours. However, it must clearly be said that this discrimination performance allows us to infer the existence of some process that generates the integration of that part of the stimulus that we would describe as an illusory contour; they cannot tell us what the animal really sees. Obviously, the alignment of stimulus fragments must be coded by the visual system without necessarily leading to the phenomenal emergence of an illusory contour. On the other hand, the alignment of edges, line-ends, or real contours is a necessary stimulus requirement for the phenomenal emergence of illusory contours (see Spillmann & Dresp, 1995, for a review). As a consequence, the visual mechanisms coding alignment are necessarily contributing to the perceptual genesis of illusory contours.

Do illusory contours reflect a visual mechanism that resolves camouflage and partial occlusion?

Biological camouflage is a naturally developed protection against visual detection by a predator. It helps to assimilate the shape of an animal to its natural environment, generally by means of a specifically colored or textured skin or fur that has evolved to conceal the contour of the animal's shape. Since camouflage exists, and fulfills a specific ecological purpose, it is reasonable to assume that there are visual mechanisms which have evolved as the ecological response to that protection, mechanisms that would permit recovery of the camouflaged outlines. Once these outlines, or contours, are detected, the effect of camouflage is cancelled out.

It has been suggested that virtual or illusory contours reveal the surface segregation process that is used by visual systems to resolve camouflage in natural environments (e.g., Ramachandran, 1987). On the basis of data from experiments with Kanizsa squares presented in stereoscopic vision (Ramachandran & Cavanagh, 1985), it has been argued that surfaces surrounded by illusory contours would 'capture' shape properties such as depth, texture, and transparency. The figure-ground separation associated with the illusory contours and the shape capture may then help to cancel out the effects of camouflage (see Figure 2).

The principle of biological camouflage is widely used by humans in situations of war, or maneuver training. Camouflage is usually only efficient if it is combined with freezing, in other words if the camouflaged animal, person, or object, does not move. The slightest movement of only a paw or an arm may make the outlines of the whole body immediately detectable and cancel out the often stunningly perfect effects of camouflage. Movement furthermore spoils camouflage by producing signals of local changes in luminance anywhere within the camouflaged surface and thus can make the object detectable without the necessity of detecting its contours.

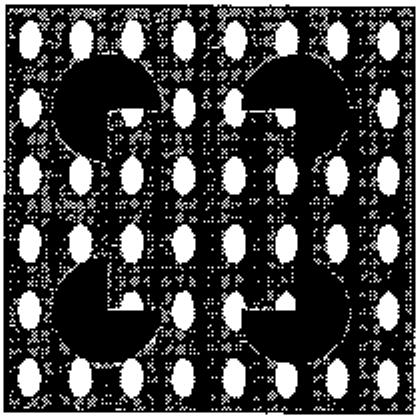

Figure 2. A figure with illusory contours suggesting transparent shape. Depth capture of the texture elements within the illusory surface is perceived.

On the other hand, a surface with an illusory contour can emerge from element motion in various stimulus patterns. Imagine a textured surface on a computer screen. Then define another surface within that texture field, a square or a triangle, for example, and make all the pixels which belong to that surface move coherently and in synchrony. What you will see in this case, is a moving square with illusory contours which appear to separate the object in motion from the background. Moving the texture elements of the background while keeping the texture elements of the virtual square stationary produces a similar effect (see, for example, Banton & Levi, 1992). These contour- from-motion phenomena have earlier been referred to as kinetic subjective contours (e.g. Kellman & Cohen, 1984), and later in terms of moving illusory contours (Mather, 1988), or motion defined contours (Banton & Levi, 1992). In species with highly developed visual systems such as non-human primates, the physiological mechanisms underlying the perception of moving illusory contours seem to involve the same cortical detectors as those that respond to moving real lines (Peterhans & Von der Heydt, 1991).

Situations where parts of objects are hidden by other objects may be considered as functionally equivalent to situations of camouflage since in both cases the recovery of contour information can be critical for solving the problem of "what belongs where" in the image plane. Evidence for the existence of a single visual interpolation process underlying the perception of partly occluded figures and figures with illusory contours comes from magnitude estimation experiments by Shipley and Kellman (1992a). They found that subjects' ratings of illusory figure clarity successfully predicted ratings for the perceived unity of structurally equivalent, partially occluded figures.

Although the existence of some intricate relationship between illusory contour formation and the visual detection of occluded or camouflaged objects is likely, the empirical data that are currently available on the topic do not allow for more than a speculative discussion. One of the problems here is that stimulus configurations with illusory contours are so complex that it is very hard to disentangle the effects of the contour as such from other, more global effects of the configuration as a whole. The aim of the following chapter is to illustrate how reducing the visual stimulus to the strict minimum required by the mechanism under investigation in a psychophysical experiment can create a context in which illusory contours are likely to be generated locally without being influenced by the global figure context. It is argued that psychophysical experiments can successfully "simulate" environmental constraints revealing the biological significance of the mechanism under investigation.

VISUAL PSYCHOPHYSICS AND MECHANISMS OF CONTOUR INTEGRATION

Recent psychophysical experiments have furthered our understanding of the visual mechanisms underlying contour perception and illusory contour phenomena by providing finely tuned measures of some of the behavioral consequences they engender. Particularly increment detection and subthreshold summation procedures have allowed to elucidate some of their functional properties in subtly tailored experiments. The extent to which the functional characteristics of contour integration may reflect underlying biological mechanisms is discussed.

Can we assess the biological significance of contour vision and "illusory" contours in psychophysical experiments?

Generally speaking, the real-world validity of any experiment on visual perception that uses pictorial representations instead of true objects is questionable. Pictorial representations *suggest* properties of real objects, but they do not *have* them. This does not mean that we should not use pictures as tools for the study of visual and perceptual processes, but it clearly means that we have to be careful with the choice of the experimental design as well as with the interpretation of the data (see also Wade & Swanston, 1990). Psychophysical methods that provide increasingly objective measures of local visual mechanisms can help to increase the general validity of pictorial stimuli in perceptual tasks.

Illusory contours, as a particular example of contour integration, have been reported to occur in pictures. What about the real world? The working hypothesis that is suggested here in this chapter claims that the perceptual genesis of virtual and illusory contours, which we can see in two-dimensional images drawn on a computer screen or on a piece of paper, must somehow be related to the ways in which the visual system builds up a coherent representation of three-dimensional form in real world images.

Threshold and subthreshold vision as a key to the functional characteristics of contour integration and the genesis of illusory contours

Psychophysical thresholds, regardless of the character of the stimulus or of the state of adaptation of the eye, are assumed to reflect constant changes of potential of a given stimulus to elicit a response in the organism. These changes of stimulus potential are independent of our knowledge about specific properties of the stimulus, and of any prior experience. They reflect measures of information processing at the earliest stages and are generally not influenced by cognitive processes, provided the psychophysical task is a true detection task.

True detection tasks are defined by either absolute detection ("yes"-"no" tasks) or by target localization (spatial or temporal alternative-forced-choice tasks). In these two cases, the detection of the visual target, regardless of its complexity, does not require the identification of the latter. In many cases it is not even necessary to identify a specific characteristic such as target orientation (e.g., Atkinson & Braddick, 1989). The only information that has to be integrated by the visual system at this level of processing is some diffuse luminance energy contained in the stimulus.

Two particularly compelling examples of finely tuned psychophysical techniques which allow to tackle the earliest stages of contour processing are light increment detection (Fiorentini, 1972) and subthreshold stimulation (e.g., Kulikowski & King-Smith, 1977). In both cases, the operating characteristics defined by the psychometric functions which relate the luminance intensity of a small light increment or a subthreshold stimulus to the percentage of correct detection can be brought into relation with the functional characteristics of visual cortical mechanisms. Two well known examples here are lateral interactions of cortical detectors triggered by luminance edges (Fiorentini, 1972), and line- or edge detector summation (Kulikowski & King-Smith, 1977). The psychophysical correlates of lateral interactions in the visual cortex are local variations in thresholds for the detection of a small light probe presented on either side of a luminance edge (Fiorentini, 1972). Line detector summation is psychophysically described by the fact that superimposing a subthreshold line on a target line of the same contrast sign reduces the detection threshold of the target line whereas the threshold is raised when the subthreshold line flanks the target line. These psychophysical observations correlate with the center-surround receptive field organization of cortical neurons (e.g., Hubel & Wiesel, 1968).

Both increment detection and subthreshold stimulation are powerful tools for the study of contour completion. They produce correlates of the mechanisms underlying the perception of contours bridging gaps between stimulus fragments. These correlates can be described as significant variations in the potential of the stimulus to elicit a response in the organism. Moreover, it is shown that these variations depend on strictly local and biologically significant factors: spatial alignment, spatial separation, length, luminance, and contrast sign, or polarity, of stimulus fragments.

The spatial alignment of stimulus fragments

In a perceptual environment of discrete visual events, the spatial alignment of points or fragments is directly related to the likelihood that these points or fragments belong to the same line, surface boundary, or object contour. Finely tuned mechanisms with a high sensitivity to alignment are thus likely to have evolved, in animal and man, to enable the visual system to detect continuity in stimuli defined by discrete points scattered in space. Moreover, we must not forget that even continuous lines are nothing but a reconstruction on the basis of discrete signals triggered in the visual system. Psychophysical evidence for the existence of fine sensitivity to alignment in man comes from a whole body of data on visual hyperacuity showing that thresholds for the smallest detectable misalignment of abutting lines are measurable in seconds of arc, and are typically smaller than the closest spacing of foveal cones (Westheimer, 1979). The functional aspect of such a high sensitivity of the visual system to the smallest of misalignments of stimulus parts becomes clearer if we think of sophisticated human activities as target shooting or walking a tight rope, for example. In some animals, high sensitivity to alignment appears to be essential for navigation behavior, as we have seen in the previous chapter.

Alignment of contour fragments is a critical parameter in most of the computational models of form vision. Contour interpolation, or the formation of illusory contours, is mechanistically achieved by adaptive, self-organizing mechanisms that allow for discontinuities in the physical input. The role of these mechanisms would be to recover the missing information via "neural bridges" built up through complex cooperative and competitive interactions between orientation selective cortical neurons (e.g., Grossberg & Mingolla, 1985; Grossberg, 1994). The principal neurophysiological support for models of this type comes from single cell recordings in V1 (Grosof, Shapley, & Hawken, 1993) and V2 (Von der Heydt, Peterhans, & Baumgartner, 1984; Peterhans & Von der Heydt, 1989; Von der Heydt & Peterhans, 1989) of the macaque monkey showing that orientation selective cortical neurons do fire when a gap separating aligned edges, lines, or line-ends is presented within their receptive field. However, knowing this still does not tell us anything about the significance of the underlying mechanisms. As long as we cannot establish a clear correspondence between model properties and specific aspects of, or changes in, behavior, we can only speculate about their functional role. In other words, if neurophysiological observations and neural models derived from them reflect functionally significant mechanisms, these latter must have a measurable correlate in the domain of visual skills or performance.

To find such a correlate, it is convenient to start with two simple questions: What is the minimal stimulus information that is needed to trigger the visual mechanism that generates a continuous contour from discrete contour events? And then, how can the output of this mechanism be measured in a specific psychophysical task? Figure 3 shows two aligned, edge-like stimulus fragments like those that give rise to Kanizsa squares with illusory contours in a complete configuration (four instead of two inducers). Contour interpolation, or illusory contour formation in the gap between the aligned edges, may require that the edge detectors activated by the inducers then activate nearby detectors that are selective to the same orientation at a collinear spatial position (see Figure 3). If this context-induced brain activity is found to engender measurable changes in a specific visual performance, then we can determine, on the basis of the nature of the behavioral changes, the functional meaning of the neural mechanism.

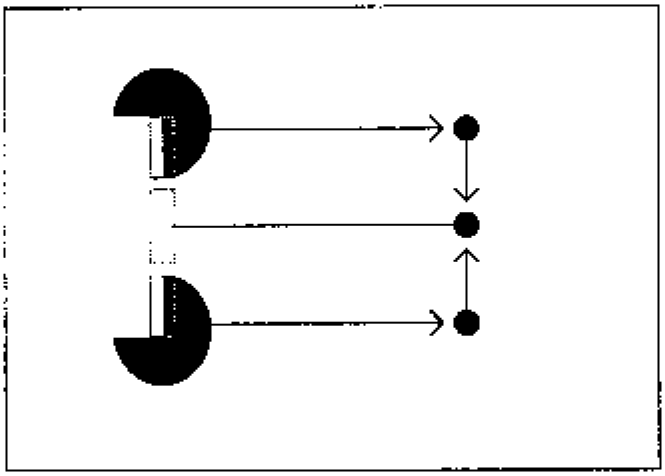

Figure 3. Edge-like boundary inducers and orientation selective neural activities triggered by the individual features. It can be assumed that the edge detectors activated by the inducers then activate nearby detectors that are selective to the same orientation at a collinear spatial position.

The idea that illusory contours may engender changes in the organism that can be measured by increment detection techniques dates back to work by Coren and Theodor (1977), Spillmann, Fuld, and Neumeyer (1984), and Jory (1987). However, these earlier attempts failed to produce a coherent set of observations for various reasons, mostly technical ones related to the type of material, and the size of the light probes used to test for local effects in illusory figures. Recent observations with highly trained observers and small test stimuli flashed on high resolution computer screens at distinct locations in illusory figures (Dresp & Bonnet, 1991, 1993, 1995) have proven the earlier intuitions right: Aligned stimulus fragments linked by illusory contours engender an increase in visual sensitivity which is spatially limited to precisely the illusory contour axis linking the ends of the physical stimuli (see again Fig. 3). This local increase in visual sensitivity finds expression in a threshold facilitation for the detection of a tiny, circular light probe (Dresp & Bonnet, 1991, 1993), and also in the observation that a non-detectable subthreshold line becomes detectable when it is presented on the axis defined by the illusory contour (Dresp & Bonnet, 1995; Dresp & Grossberg, 1995, 1997). Increment detection facilitation is dependent on alignment only, not on the visibility of illusory contours (see also Dresp, 1993, or Morgan & Dresp, 1995), the subthreshold summation effects with a line target, however, are considerably stronger in the presence of an illusory contour.

Kapadia, Ito, Gilbert, and Westheimer (1995) have measured the sensitivity to alignment of both human contrast thresholds and of superficial layer complex cells in monkey V1. It was found that a human observer's line contrast detection is significantly improved by the presence of collinear, suprathreshold context lines. The firing rates of complex cortical cells in the monkey showed the same contextual dependency on the relative location and orientation of the lines.

Alignment specific increases in visibility have also been found by Polat and Sagi (1993, 1994). The target was a Gabor pattern (a cosine patch within a Gaussian window), flanked by two collinear suprathreshold Gabor patterns. The relative visibility of the target was found to depend on collinearity, contrast, and spatial separation of the flanking stimuli. Facilitatory interactions occur when the local orientations of the target and the inducers are aligned, suppressive interactions are observed between parallel targets and inducers.

The striking modification of visual performance produced by aligned stimulus fragments and illusory contours shows that alignment and illusory contours are skill-significant phenomena, and that the biological impact of the underlying mechanisms can be defined in terms of "making the detection of visual boundaries easier". The important "warning function" that can be attributed to detection mechanisms has already been discussed in the previous chapter. Metaphorically, we could say that the visual system so to say "expects" something to occur within aligned fragments, and locally increased visual sensitivity can be seen as a goal-relevant functional consequence of alignment and illusory contours.

Variations in visual sensitivity engendered by alignment or illusory contours depend on other spatial factors that define specific contextual constraints. These include the size and proximity of aligned stimulus fragments, or illusory contour inducers.

The size and spatial proximity of fragments

If spatially aligned fragments are likely to belong to the same line, surface boundary, or object contour, this likelihood should be the higher the smaller the spatial separation of the fragments. Zucker and Davis (1988), for example, proposed that the likelihood that an array of collinear dots is grouped into a continuous contour by the visual system is directly determined by a size/spacing ratio which predicts perceived contour strength in a psychophysical rating task. Shipley and Kellman (1992b), or Banton and Levi (1992), argued similarly for edge interpolation in illusory figures on the basis of rating data suggesting that the perceived strength of illusory boundaries is best predicted by the ratio of the length of the physical contour to that length plus the spatial gap between the contour fragments (physically-specified-length to total-edge-length ratio, Shipley & Kellman, 1992b), or by a local ratio of physically specified to illusory contour length (Banton & Levi, 1992). Although a size/distance ratio as an invariant spatial determinant of contour interpolation would have the desirable ecological consequence that the formation of a perceptual unit, or contour, will not change with viewing distance, there are other psychophysical data suggesting that it may not be possible to define a unique spatial parameter for contour interpolation (see, for example, Lesher & Mingolla, 1993). This conclusion seems realistic given that there is evidence that contour interpolation does vary with viewing position or distance (Nakayama & Shimojo, 1992), and also with regard to the fact that some experiments have shown that the contrast effects engendered by inducers with different spatial separation, but identical or similar size/spacing ratio are not equivalent (e.g., Watanabe & Oyama, 1988; Dresp, Lorenceau, & Bonnet, 1990; Dresp, 1992). The fact that contrast effects strongly influence the strength of contour interpolation and its functional consequences is now well established and will be discussed in one of the next paragraphs. Spatial proximity will thus be regarded here as a factor that has an impact of its own, other variables such as size, length, or contrast of stimulus fragments being constant.

An important psychophysical consequence of the proximity of aligned stimulus fragments is that the effects of alignment on visual sensitivity diminish or change when the spacing between the fragments increases. With aligned Gabor patches, for example, the at-first suppressive effect of collinear high-contrast inducers on target detection reverses into a facilitatory effect at a critical target-inducer separation. This facilitation then diminishes when the spacing of target and inducers increases further (Polat & Sagi, 1993, 1994). Moreover, the dependence of sensitivity enhancement on alignment and spatial separation was found to be invariant across different global orientations, including curves (Polat & Sagi, 1994). In figures with illusory contours, increasing the gap between two collinear inducers decreases facilitatory effects on the detection of a small light increment presented on the illusory contour (Dresp & Bonnet, 1991, 1993), and facilitation disappears completely at a target-inducer separation of about 1.75 degrees of visual angle with Kanizsa square inducers of constant size. Furthermore, suppressive effects reflected through local threshold elevations observed near the borders of the inducers at locations away from the alignment axis, or illusory contour, decrease with increasing inducer spacing (Dresp & Bonnet, 1993).

Figure 4 shows figures with illusory contours and the same inducer length/spacing ratio. It illustrates that the lateral separation of the round borders of the inducing elements varies even when the real-to-illusory or real-to-total contour ratio is constant. The size/ratio hypothesis (e.g., Shipley & Kellman, 1992b; Banton & Levi, 1992) thus neglects the possibility of an influence of lateral interactions further away from the axis of alignment on contour grouping or illusory contour formation. This may explain some of the discrepancies in the data from different rating experiments (Banton & Levi, 1992; Shipley & Kellman, 1992b, Lesher & Mingolla, 1993).

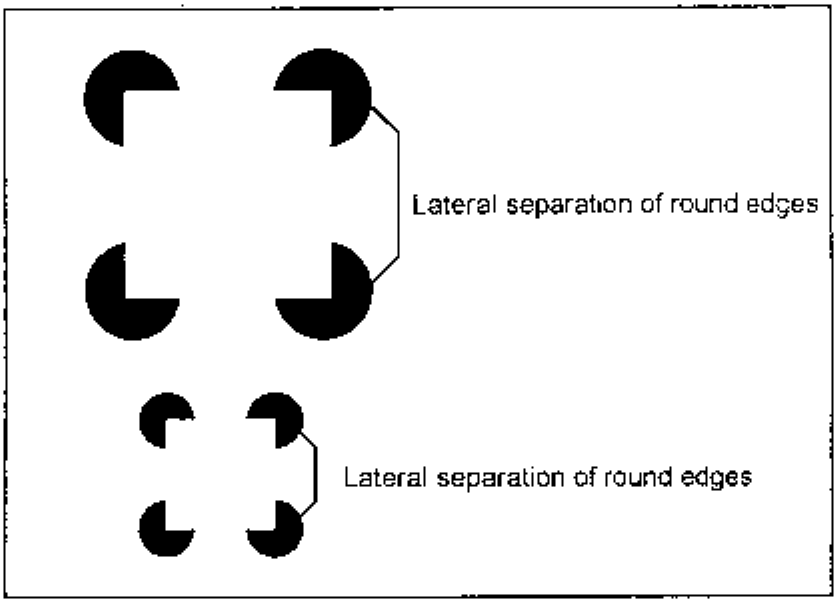

Figure 4. Relative contour/inducer length is not the only determinant of contour interpolation. This figure shows two Kanizsa squares with identical real-to-total and real-to-illusory contour length ratio. The lateral distance between the borders of the inducers is, however, not the same. Psychophysical thresholds have shown that lateral contrast interactions are an important factor in illusory contour integration (e.g., Dresp & Bonnet, 1993)

Lateral suppressive interactions, also observed by Polat and Sagi with Gabor stimuli, are functionally as significant as the facilitatory interactions observed on the axis of alignment, or on illusory contours. Lateral interactions may determine contour grouping in the sense that information in the regions immediately adjacent to the contour axis, but not belonging to the contour tends to be suppressed by the visual system. One of the psychophysical consequences is that the detection of luminance stimuli that are not contour-relevant becomes significantly harder. Attention and relative viewing position should have an influence on spatial interactions upon and alongside the contour axis, and further psychophysical research is clearly needed here to evaluate these biologically highly relevant parameters (see also Nakayama & Shimojo, 1992).

Other significant factors that determine contour integration are the relative visibility of aligned fragments and the sign of contrast they carry. Both have been found to engender measurable consequences on contour interpolation and the formation of illusory contours.

Contrast intensity and contrast polarity

The visual system is particularly sensitive to differences in relative visibility rather than to differences in absolute luminance. Relative visibility of contour fragments matters especially when the background of the surface or the object delineated by them contains the same or similar fragments, in other words, when a surface and the background have the same or similar textures.

High-contrast fragments are generally found to mask nearby collinear target stimuli, whereas low-contrast fragments facilitate target detection (e.g., Polat & Sagi, 1994; Mc Court & Paulsen, 1994; Morgan & Dresp, 1995). This psychophysical observation can be related to biological responses to environmental constraints. In a natural visual environment, high contrast stimulation does not represent a problem or a situation of specific constraint. High-contrast stimuli *per se* may only be suitable for testing some of the limits of the visual system in lab situations. The biologically critical situations with regard to vision and visual function are likely to occur under low-contrast conditions, or bad visibility in general. Thus, it is not surprising at all that early visual grouping, or the formation of illusory contours, works best with inducers in the low-contrast range.

When the contrast sign, or polarity, of aligned fragments varies, contour interpolation may still be possible in some critical conditions. Zucker and Davis (1988) have shown that rows of dots are unlikely to be grouped into lines by the visual system when the contrast sign of the dots alternates within a given row. Contour interpolation does, at a first stage, require the grouping of local contrast provided by fragments carrying the same sign. This was also found in experiments by Dresp, Salvano-Pardieu, and Bonnet (1996), showing that illusory contour formation is possible when the inducing lines are rows of dots or dashes, but not when the dots or dashes carry alternating contrast signs. When the constraint of local homogeneity of contrast signs is satisfied, contour completion, or illusory contour integration, is possible across polarities. Figure 5 shows phenomenal examples illustrating this point.

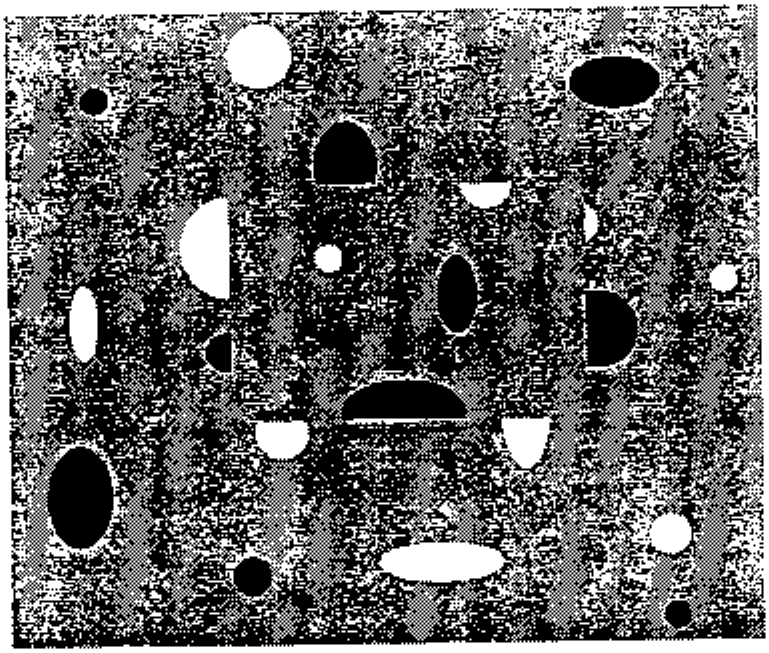

Figure 5. A "camouflaged" square the contours of which can be detected on the basis of the alignment of edge fragments. Variations in contrast intensity or polarity have little effect on perceived alignment or induced shape (e.g., Dresp, Salvano-Pardieu, & Bonnet, 1996).

One generally observes a striking difference in the quality of illusory contours (see also Prazdny, 1983) when comparing figures with inducers carrying only one polarity to figures with inducers carrying opposite polarities: The contours in the latter look much sharper. In the case of the Ehrenstein figure, the shape of the illusory surface is usually ambiguous when the inducing lines all have the same contrast polarity (see also Day & Jory, 1980), but this ambiguity is completely resolved when the inducers have opposite signs. A diamond-shaped surface with sharp boundaries emerges from the center of the configuration (Dresp, Salvano-Pardieu, & Bonnet, 1996). Thus, contour interpolation across polarities is the result of a set of mechanisms with the specific functional role of reducing contextual ambiguity.

Here again, the effects of the underlying visual mechanisms can be measured psychophysically and interpreted in terms of goal-relevant behavioral operations. When a small subthreshold line, not detectable when presented out of context, is flashed on an illusory contour induced by edge fragments of opposite contrast polarity, it becomes detectable. The effect increases with increasing intensity of the line, all levels being 'subthreshold' when detection of the line is measured out of context. This summation between the stimulus energy carried by the illusory contour and the energy carried by the target line is correlated with an increase in the perceived strength of the illusory contour. However, if the target line is fractioned, and the contrast sign of half the line does not match the contrast sign of the nearest inducer, all the facilitatory effects are destroyed (Dresp & Grossberg, 1995, 1997). The disposition of the visual system to extract contour information is thus directly determined by local contrast signs carried by the contour fragments. A significant interaction between contrast polarity and contrast intensity of contour fragments has been found by Wehrhahn and Dresp (1996, 1997). At low contrast intensities, only targets and inducers of the same contrast sign produce detection facilitation whereas at high contrast intensities, only inducers of opposite contrast sign (with regard to the target) facilitate the detection of a collinear target.

This differential sensitivity of the visual system to particular combinations of contrast intensities and signs along the axis of a contour could very well reflect the "smart" mechanisms which help to detect camouflaged contours or resolve shape ambiguities. Under conditions of low-contrast, or bad visibility, a system that exclusively groups or filters information carrying the same sign or color may be more efficient in recovering the global shape of an object. When visibility is good, or contrast high enough, filtering information of different sign or color may allow to recover increasingly detailed shape information. Models based on first-and second-stage visual filters, or channels, can successfully account for some of the effects of contrast intensity and polarity on visual spatial groupings (e.g., Zenger & Sagi, 1996).

CONCLUSIONS

The current neural models of early visual grouping are conceived on the basis of functional hypotheses concerning the role of local stimulus characteristics such as alignment, inter-element gap, element size, contrast, and contrast polarity. However, the fundamental epistemological challenge for neurophysiologists, psychophysicists, and the modeling community altogether remains to establish an increasingly finer correspondence between the functional properties of models and functionally significant changes in visual performance or behavior. Our understanding of the functional characteristics of mechanisms responsible for contour interpolation or the perception of illusory contours taken as an example here can be furthered on the basis of behavioral observations made available through increasingly fine psychophysical probing. Psychophysics with human observers presents certain advantages compared to neurophysiological techniques, though both approaches are clearly complementary, for relatively simple reasons. There is an important difference between observers and neurons that often seems to be neglected likewise by neurophysiologists and modelmakers: observers can be instructed. They can be told which attributes of the stimulus to respond to and which to ignore, and they can be trained to do some tasks more or less automatically. This also holds to a given extent for animals. Comparative psychophysics (e.g., Zocke, Sarris, & Hofer, 1989) allows for testing hypotheses of biologically relevant visual and perceptual mechanisms by determining species-specific distinctions in how a given perceptual variable affects performance. The fact that interpolated, or illusory contours do not only affect human visual performance but also that of various animals with structurally and functionally different visual systems (see also O'Carrol, 1993) challenges the classic cognitive conceptions and the most recent cortical models of contour integration across space likewise. It seems as if our various conceptions of perceptual processes we believe to be involved in the genesis of illusory figures might have to be reconsidered. Since everything we see is, after all, nothing but a reconstruction on the basis of information generated by complex interactions between light and matter, it may not make any sense at all to call the perception of physically non-specified borders or surfaces "illusory". "Illusory" contours and shapes have been dealt with as "exceptions to the perceptual rule", occurring only in very particular configurations of stimuli, for quite some time. However, they can emerge quite often as rather unsurprising parts of a scene represented in a pictorial black-and-white line drawing like the one shown in Figure 6, featuring a famous engraving by M. C. Escher ("Rêve", 1935).

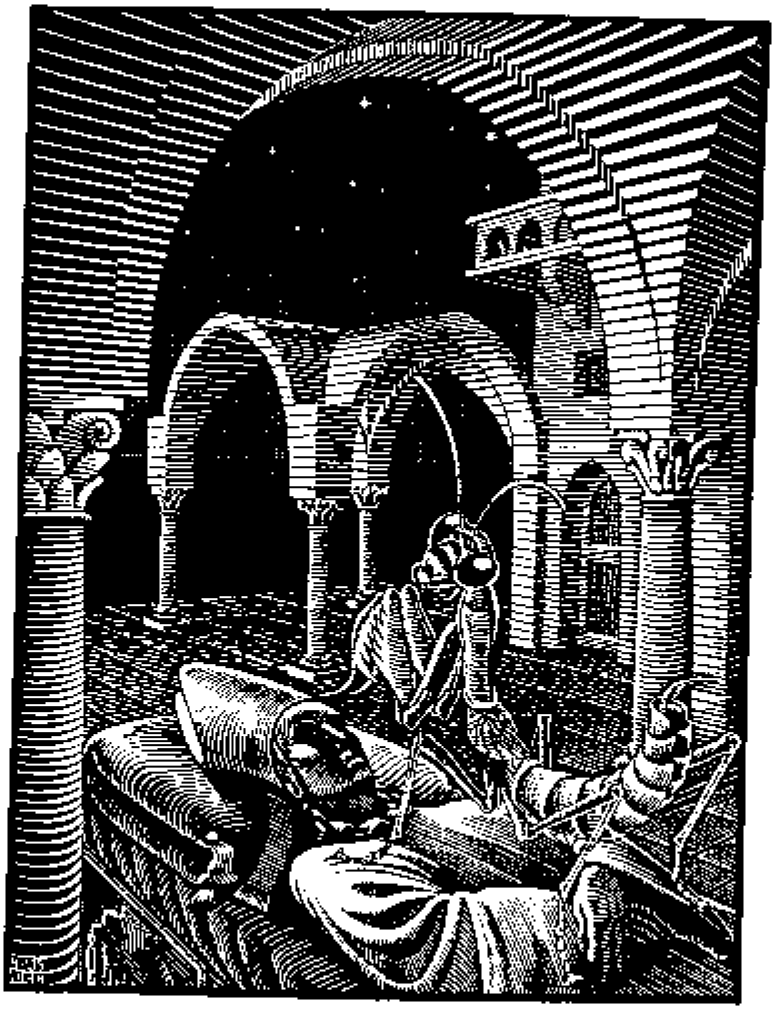

Figure 6. This engraving by M. C. Escher (1935), "Rêve", strikingly illustrates how naturally "illusory" boundaries are perceived and integrated as essential parts of the image. The pictorial representation shows two- dimensionally oriented black/white contrasts only, the percept, however, is utterly complex.

"Illusory" contours can pop out at unsuspecting observers from scenes, pictures, or images without time for a thorough analysis of the stimulus, and the idea that their genesis takes place quite early in the chain of visual processing has now become a widely accepted working hypothesis.

Studying the perception of illusory contours as a matter of perceptual or visual skills has not been envisaged by many authors, apart from Gellatly (1982), or more recently Nakayama and Shimojo (1992). The advantage of a psychophysical analysis of these phenomena in such terms is that it allows us to get away from the physiology/cognition dichotomy and to assimilate contour perception, or the perception of illusory contours, to skills in general (Gellatly & Bishop, 1987). Given that we now know so much more of the visual system and its functional implications in grouping processes, it has become possible to approach quite complex perceptual phenomena from the bottom of their genesis. This bottom-up approach has the advantage of being close to the biological reality of the mechanisms under investigation and has opened new doors in the sense that we no longer have to theorize about questions like perceptual grouping *in abstracto*, as in the times of the early Gestalt approaches when it was still impossible to relate general perceptual principles to clear hypotheses of brain-behavior functions.

RÉSUMÉ

Des données récentes en neurophysiologie et en psychophysique ont suggéré que la perception des contours illusoires chez l'homme et chez l'animal repose sur des mécanismes précoces d'intégration des informations locales du stimulus par le système visuel. Ces mécanismes sont parfois supposés avoir une fonction spécifiquement adaptative et leur signification pour la survie d'espèces variées a été discutée. Les travaux expérimentaux et les approches computationnelles sur le phénomène des contours dits "illusoires" nous ont amenée à les comprendre comme étant fonctionnellement équivalents aux contours "réels". Cet article propose une revue de question des principales données et de quelques arguments théoriques en faveur d'un tel point de vue et amène à un exposé de quelques enjeux théoriques et méthodologiques visant à montrer dans quelle mesure les mécanismes sous-jacents aux contours "illusoires", ainsi que leur fonction adaptative, peuvent être mis en évidence

par des techniques fines de mesures psychophysiques chez l'homme et probablement chez certains animaux.

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