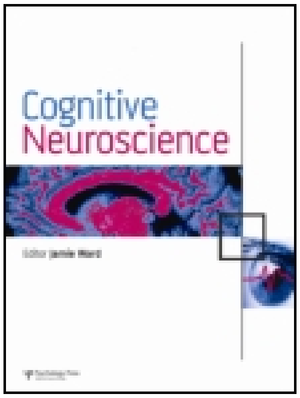

Cognitive Neuroscience
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/pcns20

Surface reconstruction, figure-ground modulation, and border-ownership

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Version of record first published: 15 Feb 2013.

To cite this article: Danique Jeurissen , Matthew W. Self & Pieter R. Roelfsema (2013): Surface reconstruction, figure-ground modulation, and border-ownership, Cognitive Neuroscience, 4:1, 50-52

To link to this article: http://dx.doi.org/10.1080/17588928.2012.748025

COGNITIVE NEUROSCIENCE, 2013
Vol. 4, No. 1, 31–61, http://dx.doi.org/10.1080/17588928.2012.727387
(includes Discussion Paper, Commentaries, and Reply)

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Taylor & Francis Group

Discussion Paper

The “side” matters: How configurality is reflected in completion

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The perception of figure-ground organization is a highly context-sensitive phenomenon. Accumulating evidence suggests that the so-called completion phenomenon is tightly linked to this figure-ground organization. While many computational models have applied borderline completion algorithms based on the detection of boundary alignments, we point out the problems of this approach. We hypothesize that completion is a result of computing the figure-ground organization. Specifically, the global interactions in the neural network activate the “border-ownership” sensitive neurons at the location where no luminance contrast is given and this activation corresponds to the perception of illusory contours. The implications of this result to the general property of emerging Gestalt percepts are discussed.

Keywords: Figure-ground; Depth order; Illusory contour; Illusory surface; Modal and amodal completion; Border-ownership; Gestalt; Emergent property.

When one sees an image in Figure 1, one perceives a central white surface on top of the surrounding black objects. It is facilitated by the accompanying illusory contours and the “brightness illusion” effect (in this example, the color of the central surface is perceived as lighter than the background). This phenomenon is called “modal completion” because the central surface is perceived clearly despite the fact that some of its parts are not physically defined in the image.

How does our visual system create this perception? The phenomenon has often been described in the framework of a “contour-completion and filling-in” mechanism: Extra lines are added to the gaps between pairs of aligned borderline segments and the enclosed area is filled-in with surface qualities. However, how does the brain detect the gaps of borderlines and determine to fill-in the gaps? Moreover, is this really what happens in the brain in the first place? It is important to investigate the underlying mechanisms for completion, not only at the phenomenological level, but also at the level of the neural machinery in the visual cortex.

After more than half a century of investigation, do we really know how completion is created? Surprisingly, the answer is “no”. The aim of this paper is to reveal and discuss the fundamental problems (and confusions) in investigating the completion mechanisms. In addition, we explain the advantage of an alternative view to explain the phenomenon by the context–sensitivity (the Gestalt nature) of our perception, based on the neural mechanisms that reflect the global configuration of the different components available in the image. We first analyze the completion phenomenon and discuss the fundamental problems in investigating its underlying mechanisms.

An important contribution toward understanding the mechanism of completion was made by Kanizsa (1955), who published his famous image of an “illusory triangle,” now known as the “Kanizsa triangle”

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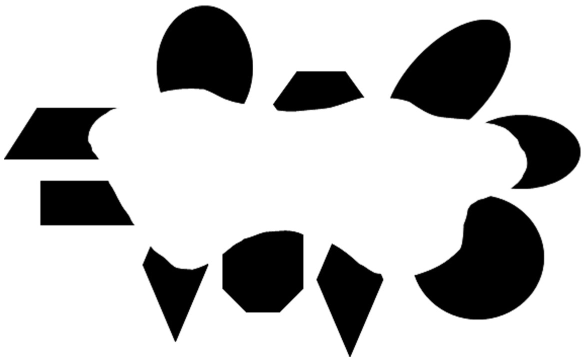

Figure 1. In this image, the central white area is perceived as a surface occluding the surrounding black objects. Furthermore, the central surface is perceived as lighter (brighter) than the background.

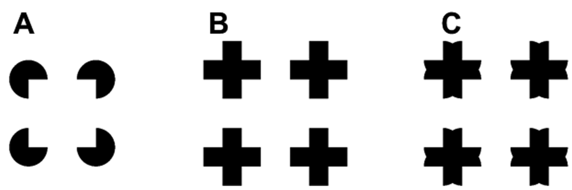

Figure 2. A: Kanizsa illusory figure. B: Non-illusory variation of the Kanizsa figure. Although the borderlines surrounding the central square area are exactly the same, the perception of the illusory surface is strongly suppressed by the modification of the shape of the surrounding objects. C: Even if the contour shapes of the crosses are modified to match the curved part of the pacmen in A, the figure is still non-illusory.

(modified to a "Kanizsa square" in Figure 2A). Since its publication in 1955, this image has been a key tool in the investigation of fundamental properties of the visual system. The advantage of this simplified figure is that the shapes of the surrounding objects ("inducers") can be changed to examine its effect on our perception. An example with a striking contrast to the original image is the non-illusory variation as shown in Figure 2B. With this modification, the illusory perception seems to disappear (or becomes significantly reduced). Thanks to the Kanizsa image, systematic modifications are made possible, and factors that are potentially involved (or not involved) in the underlying mechanisms can be investigated.

Another important contribution that sheds light on the underlying mechanism of completion was introduced by von der Heydt, Peterhans, and Baumgartner (1984). They reported that neurons in V2 respond when their receptive fields are located at the place where illusory contours are perceived (von der Heydt et al., 1984). Since then, such neurons in V2 (and some in V1) have been reported by many laboratories (Grosof, Shapley, & Hawken, 1993; Lee & Nguyen, 2001; Peterhans & von der Heydt, 1989; Ramsden, Hung, & Roe, 2001; Sheth, Sharma, Rao, & Sur, 1996; von der Heydt & Peterhans, 1989a). The discovery of these neurons means that we have the actual entity at hand that must be part of the machinery creating the perception of the illusory contour. Finding out exactly how the activities of these neurons are produced is the central issue in understanding why and how the completion phenomenon emerges.

In the neuro-computational models aimed to mimic the Kanizsa illusion, convolution filters or algorithms specifically designed for detecting the collinear (or curvilinear) alignment of the borderlines were implemented to complete the gap between them, and the surface property was filled-in later ("contour-completion and filling-in"). We will point out the problems and inconsistencies of this common approach and we will argue that the function of the neurons active at the illusory contours is not to simply detect the collinearity. Instead, we argue that these activities are the result of a border-ownership computation reflecting the global configuration of the image. The requirement of the border-ownership computation means that the depth order of the surfaces on both sides of the boundary has to be determined. The importance of the depth order or figural side in perceiving the illusory contours has been pointed out (Coren, 1972; Gregory & Harris, 1974; Nakayama, Shimojo, & Silverman, 1989) and the depth-order computation reflecting the configurality has been implemented in several models to reproduce the illusory contour perceptions (Finkel & Sajda, 1992; Geiger, Pao, & Rubin, 1998; Kogo, Strecha, Van Gool, & Wagemans, 2010; Sajda & Finkel, 1992; Williams & Hanson, 1996). If this is correct, the neural signals at illusory contours should be interpreted as the signals indicating the existence of the (illusory) surface by the depth order at the location of the illusory contours, as opposed to the conventional interpretation that the signals are to indicate the borderline. This viewpoint is not only important to explain the completion phenomenon, but also has significant implications to the neural machinery in general which reflects the global properties of the image and provides a tool to investigate how Gestalt properties such as configurality and relational properties of our perception emerge.

In the following sections, we first show some problems of the conventional explanation of completion, followed by the alternative explanation we offer. We then discuss the implications of this view in neurophysiological terms.

PROBLEMS: INCONSISTENCIES IN THE "LINE-DRAWING" APPROACH

Hubel once pointed out the following "paradox": "Many people, including myself, still have trouble accepting the idea that the interior of a form . . . does not itself excite cells . . . [O]ur awareness of the interior . . . depends only on cells sensitive to the borders . . ." (Hubel, 1988, p. 87). While neurons seem to show responses only at boundaries, how is the "interior" of the surface coded in the neural system? The paradox originates from the very view that these neurons are boundary detectors. In this view, the neural responses are seen as part of a "line-drawing" process along the boundaries. In this section, we will point out that this "line-drawing" view is not a correct way to interpret the neural activities at boundaries and does not explain the completion phenomena consistently, and we will discuss an alternative interpretation of these neural activities in the section that follows.

An explanation of completion based on collinearity detection

In Kanizsa's illusory figure (Figure 2A), because the central illusory surface is perceived as accompanied by a "complete" contour, this phenomenon is called "modal" completion. (Note that completion is called "amodal", on the contrary, if a missing contour is supposedly completed behind an occluder such that the completed contour is not directly visible. For a further discussion of these terminologies, see Michotte, Thinès, & Crabbé, 1964. We will discuss amodal completion later in this paper.) Many attempts to explain the mechanisms behind this phenomenon have focused on "contour-completion", and developed a "line-drawing" algorithm based on collinearity detection of the boundaries (e.g. Grossberg, 1994; Grossberg & Mingolla, 1985a, 1985b; Ullman, 1976). In these approaches, the alignment of the two boundary elements is detected and the elements are extended to fill the gap between them. As we point out later, however, for a signal to be called a contour signal, the surface represented by the contour has to be specified. This means that it has to be indicated on which side of the borderline the represented surface exists. Because the aforementioned process of bridging two boundary elements itself is irrelevant to detecting the existence of an illusory surface, it should be called "borderline-completion" (see Line, borderline, contour section for more details regarding the definitions of these terms). Here, we show some examples to indicate why and how this "line-drawing" approach is problematic.

Let us consider again the images shown in Figure 2. Importantly, the collinearity-based approaches encounter a problem as soon as the non-illusory figures are considered (Figure 2B, 2C). The cross objects in Figure 2B have straight borderline segments just as in the original Kanizsa figure, but the completion is not perceived as in Figure 2A. Furthermore, replacing the straight contours on the side of the cross objects with the curved ones, as in the pacmen (Figure 2C), does not lead to a recovery of the illusion. These examples indicate that the particular relationships between the curved contour and the straight contour of the pacmen is not the cause of the illusion; this argument also applies to the "orientation-competition" between the intersecting borderlines (Grossberg & Mingolla, 1985a, 1985b). From these arguments, we can conclude that our perception of modal completion cannot be explained consistently by the collinearity detection principle.

The underlying problem is in creating borderlines without considering the side of the surface that they should represent if they were contours. If the process were to complete borderlines, it would be independent of a particular surface on one side of the boundary. If, on the other hand, the contours are completed to define (illusory) surfaces, the process should be tightly linked with the underlying mechanisms of the perception of the central surface (Figure 2A but not in 2B and 2C).

The problems of the borderline-completion approach also become apparent when "amodal completion" is considered. It has been suggested that amodal completion may share the underlying mechanisms with modal completion (the so-called "identity hypothesis"; see Kellman & Shipley, 1991). If the same problems of the "line-drawing" are found in amodal completion as explained below, these constitute general problems of the borderline-completion approach.

Let us consider here hypothetically that we are trying to develop an algorithm to reproduce this phenomenon with a collinearity-based completion approach. An example of amodal completion is shown in Figure 3A: An object (the straight line in this example) is perceived as being occluded by another object (rectangle) and the occluded part is perceived as continuing behind the occluding object. It would be possible to create an algorithm that would work to complete the two line segments (* and **) by extending the two endpoints. In Figure 3B, a continuation of edges of a large rectangle behind the other rectangle may be perceived. If this is the case, to reproduce this continuation of the edges, the above algorithm needs to be modified already because what continues behind the frontal gray rectangle is not a line-like *object* as in Figure 3A but the *contour* of the black rectangle. The algorithm,

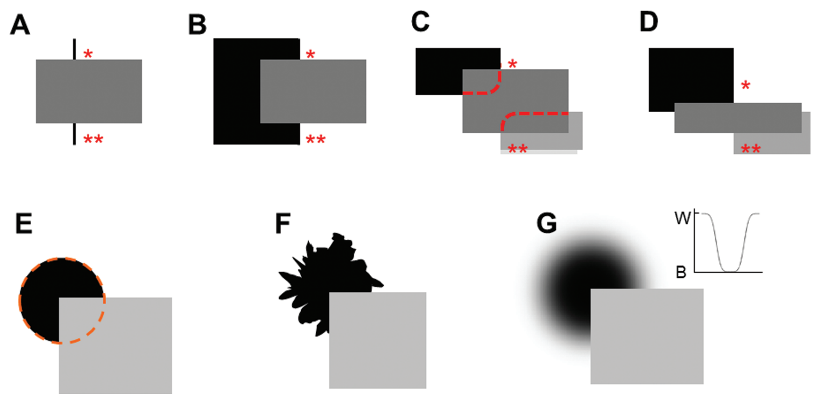

Figure 3. Examples of amodal completion. In A and B completion occurs between the collinearly aligned contours (* and **). In C, although the size and alignment of the two contours are exactly the same as in B, they are separated and completed with individual rectangles. This result cannot be explained by the longer distance between the two aligned contours compared with the distance to the contours of the individual rectangles because, as shown in D, even if the distance between the two line segments is shortened, they do not become completed in our perception. In the images shown in E, F, and G, the black objects are perceived as being occluded by the gray rectangles. Only in the case of E, it is possible to draw a completed contour behind the rectangle. In F, the shape of the black object is arbitrary and hence it is not possible to draw a completed contour, although we perceive completion of the black surface. In G, the edge of the disk is smoothed (the profile of the grayscale value of the object is shown in the inset. W: white, B: black). In this case, it is also not possible to draw the completed contour, although the surface is perceived to continue behind the rectangle.

then, has (1) to detect the boundaries of surfaces, (2) to create a borderline map of the image and (3) to complete the gap between the two aligned borderlines (* and **). It is possible that this modified algorithm is able to reproduce the completion in both Figure 3A and 3B consistently.

However, let us consider the image shown in Figure 3C. Although the two aligned contours have exactly the same physical dimensions as in Figure 3A and 3B (* and **), the completion between them is not perceived. Apparently, this cannot be explained by collinearity. One may, then, attempt to further elaborate the approach by assuming that the co-curvilinear alignment (orange dashed lines) is detected *and* that the distance between the line segments is taken into account. For example, a curvature minimization algorithm (Ullman, 1976), a random-walk algorithm (Williams & Jacobs, 1997), entropy measurements, or an energy minimization algorithm may be implemented to complete them in this way. The distance between the two line segments can be, however, shortened as shown in Figure 3D without leading to their completion in our perception.

Furthermore, if a disk is occluded by a rectangle as shown in Figure 3E, the disk is perceived to continue behind the rectangle. With a co-curvilinearity-based approach, the contour of the disk (dashed line) may be extended. However, if the shape of the occluded object is arbitrary, as shown in Figure 3F, this approach is no longer applicable. On the one hand, we perceive the continuation of the object's surface vividly, but on the other hand, we are not able to draw an exact contour of the surface behind the rectangle. Furthermore, this approach faces a serious problem when there are no contours to extend in the first place, as in Figure 3G.

As such, it would be nearly impossible to reproduce our perception in all these examples by a consistent algorithm with the co-(curvi-)linearity-based approach. Why is this approach not working? Psychophysical experiments provide a hint regarding the fundamental problem with this approach, as discussed next.

The "side" matters: The influence of figural surfaces

In the previous section, we pointed out the difficulties with the borderline-completion approach. We called it "borderline-completion" but not "contour-completion" because this type of line-drawing approach does not consider, in the process of completion, the side of the surface that the completed contour would represent. Here, we explain that this line-drawing approach cannot match our perception, in principle, because the shapes of modally and amodally completed contours are affected by the side of a boundary on which we perceive a figural surface (a surface closer to the viewer than the surface on the other side and hence perceived as figure). If a mechanism of completion aims to extend lines in gaps between borderlines, it would be done in a borderline map such as shown in Figure 4A. However, as shown in Figure 4B, these borderline segments may be parts of the diamond behind the oval or, equally possibly, they may be parts of an L-shaped polygon as

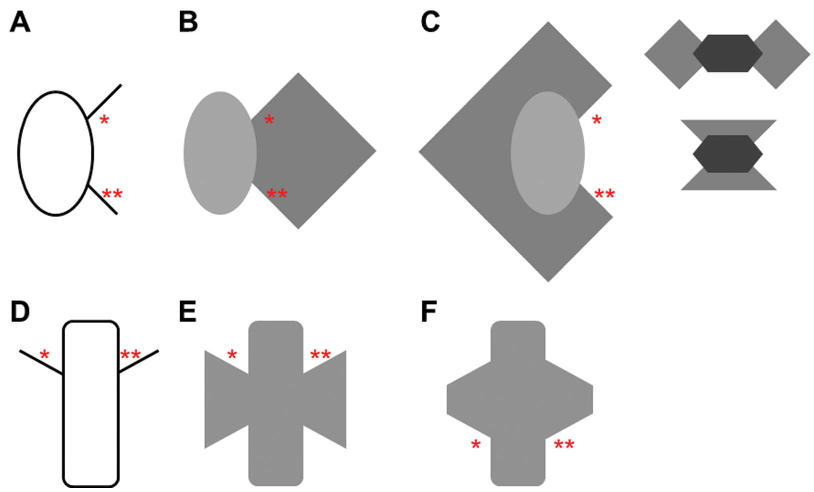

Figure 4. A: Co-curvilinearly aligned borderline segments (* and **). This borderline map may be created from an image as shown in B with a diamond shape occluded by the oval or as shown in C with an L-shaped polygon occluded by the oval. The question is whether the completed contours are the same in B and C. Inset: Similar configurations as used in Fantoni et al. (2005). D: Another pair of co-curvilinearly aligned borderline segments (* and **). If the surfaces in images E or F are presented with stereoscopic equipment so that the central surface is perceived as being farther than the side surfaces, the contours marked by * and ** are modally completed. In terms of co-curvilinearity, the alignments of the line segments are exactly the same in E and F. Empirical data showed that the difference between the configurations of these images influenced the perceived illusory contours.

shown in Figure 4C. The difference is that the figural surface exists on the right side of the completed borderline in B or on the left side in C. Does the difference of the side of figural surfaces affect our perception of completion? Psychophysical experiments have shown that this is indeed the case. Fantoni, Bertamini, and Gerbino (2005) used two images that create partially identical borderlines but one of them has two occluded (amodally completed) surfaces on the left and the right sides of a central occluder (similar to Figure 4C inset top), while the other image has two figural surfaces on the top and the bottom of the occluder (Figure 4C inset bottom). Their experimental data clearly showed that the perception of the amodally completed contours differed in their positions between these two images. Note that the borderline segments that intersect with the occluder are the same in these two images. When the gap between the segments is completed, however, the results are different. Therefore, an important conclusion can be drawn from the results: The perception of the completed contour depends on the *side* of the contour on which the occluded surface is present.

Fulvio and Singh (2006) also showed a similar effect of the “side” of occluding (modally completed) surfaces. They used stereoscopic equipment to present images similar to those shown in Figure 4E and 4F. In their experiment, the central vertical shape was placed further from the viewer and the two surfaces on the side closer to the viewer. In this configuration, the two side surfaces were modally completed. Note that the pair of boundary segments marked by * and ** are aligned in the vertical position and they intersect with the central surface with the same angles in both images. Therefore, they have exactly the same quality of co-curvilinearity. The difference between the two images is whether the figural surface is concave or convex. The positions of the perceived contours of these occluding surfaces differed once again: The convex shape (F) created smoother contours than the concave shape (E).

Although these data may be explained in other ways, a straightforward interpretation of the results is that the completion process is tightly coupled with the perception of surfaces. The completion is not the result of two separate processes—the line-drawing and the filling-in of surface qualities. The process of surface construction and the process of contour completion are tightly linked to each other.

These examples indicate that the collinearly aligned contour segments themselves (* and **) do *not* carry enough information to fully reproduce our perception. In fact, Tse (1999a, 1999b) argued, by showing various elaborate images, that aligned contours do not always create a completion. Therefore, a large number of mathematically elegant models proposed within the line-drawing approach (e.g., Fantoni & Gerbino, 2003; Kalar, Garrigan, Wickens, Hilger, & Kellman, 2010; Kellman & Shipley, 1991; Ullman, 1976; Williams & Jacobs, 1997) would face serious difficulties to create line-drawings behind occluding surfaces to reproduce the dependency of contour completion on the “side-of-the-figure”. Nevertheless, this is the most commonly practiced approach found in literature. If these counter-examples point out fundamental problems of this approach, this way of thinking of completion mechanism has to be abandoned, and an alternative view is needed.

In fact, some papers showed that the perception of depth order or 3-D configuration plays the fundamental role in the completion phenomenon (Anderson & Julesz, 1995; He & Nakayama, 1992; Nakayama, He, & Shimojo, 1995; Nakayama & Shimojo, 1990, 1992; Nakayama et al., 1989; Tse, 1999a, 1999b). Importantly, the determination of depth order is highly context-sensitive. The question is, then, how is the side of figural surfaces determined in the completion process? In the next section, we argue that algorithms tuned to construct surfaces reflecting the global configuration of the image can explain the underlying mechanism of completion.

SOLUTION: BORDER-OWNERSHIP COMPUTATION AS PART OF A SURFACE CONSTRUCTION PROCESS

The surface is what is to be completed

The examples shown above (Figures 2 and 3) indicate the problems of the "line-drawing" approach. Let us, then, step back a moment and re-examine our perception of completion when we see these examples. The most prominent effect of these images on our perception is a vivid sense of the existence of a surface. In the examples of modal completion (Figure 2A), we perceive the illusory surfaces occluding the surrounding objects. In the examples of amodal completion (Figure 3), the continuation of surfaces behind the other (occluding) surfaces is perceived while the continuation of the borderlines is not always observed. This suggests that the mechanism involved in completion is tuned to constructing surfaces. (Note that even the line in Figure 3A is, in fact, a 2-D object with an extremely narrow width.) The problem with aiming to draw a line could be that it does so without reflecting 2-D configurality. When a contour appears to complete, it may happen because the existence of surfaces is emerging through the processes involved in the computation of completion. In addition, it is possible that the completion of a contour happens only in special cases when the edge of the surface is clearly defined by the process (instead of having smooth edges in which case the salient surface is still perceived without contours; see Stanley & Rubin, 2003). Once viewed as such, the completion phenomenon may be the result of processes that aim to (re-)construct surfaces and the illusory contours may emerge through this computational process as the edges of the surfaces.

Before discussing how such process is accomplished in the visual system, we must point out that the failure to understand the fundamental insight described above has led to considerable confusions regarding the definitions of fundamental terms commonly used in perception research, such as line, border and contour. This confusion has been ignored for many years in the perception research community and the usage of poorly defined terms has been a common practice. It is essential to remove this confusion because it has led to problems in explaining the perceptual mechanisms and in interpreting the neural activities as representing these concepts.

Line, borderline, contour

Consider the concept of a line first. The term "line" is used in two different ways. In geometry, a line is "a straight or curved continuous extent of length without breadth" (Allen, 1990, p. 688). We will refer to this as definition #1. The mathematical definition of line without a width differs from the "line" used in daily life where it usually refers to an elongated rectangular surface with a very narrow width. This corresponds to another definition of "line" as "a continuous mark or band made on a surface" (Allen, 1990, p. 688). We will refer to this as definition #2. As trivial as it may sound, this difference between the two definitions has significant implications in understanding perception. Note that both conditions can occur in reality. Let us consider the example shown in Figure 5A. When two surfaces with different qualities abut, a "line" is created at the location where the two surfaces meet. This line does not have a width and hence it is a line as per definition #1. On the other hand, a line-drawing as in Figure 5B consists of a line as per definition #2. It is an essential first step to recognize and distinguish these two definitions.

This example also indicates the problem with the definitions of "boundary" and "borderline". In Figure 5A, a boundary exists between two surfaces where they abut (without a width, definition #1). The line drawn in Figure 5B (definition #2) signals the existence and location of the boundary in Figure 5A. This is, then, the *representation* of the boundary, not the boundary itself. This is what *borderline* is: A *borderline* is "a line marking a boundary" (Allen, 1990, p. 128). We often need to indicate the location where two areas are divided (e.g., drawing a map without or with country borders, Figure 5C and D, respectively). When we need to indicate where they are divided, we

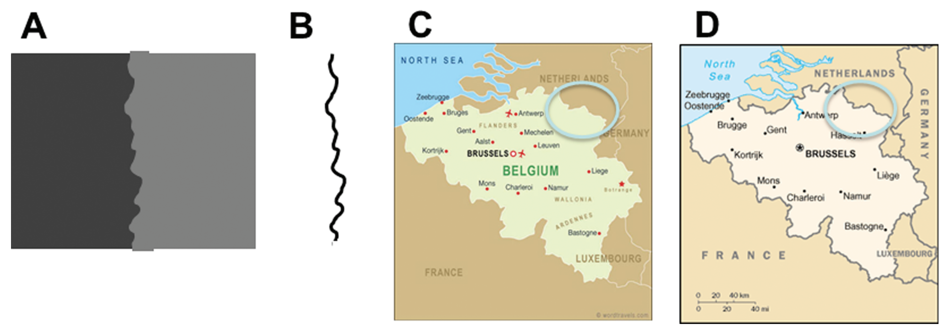

Figure 5. Two different kinds of "lines". A: A boundary created by two abutting surfaces (definition #1 in text). B: The representation of the borderline in A by a line-drawing (definition #2 in text). Examples of "line" in definition #1 (C) and #2 (D) in country maps.

often draw lines quickly (Figure 5B) instead of drawing two surfaces with different qualities (Figure 5A). In doing so, however, we should recognize that we are using a representation of the boundary, not the boundary itself, for communication purposes.

The term "contour" should also be used with caution. A *contour* is "an outline, esp. representing or bounding the shape or form of something" (Allen, 1990, p. 249). When there is a sudden change of surface properties such as luminance, color or texture, the location of the change becomes a boundary, which can then be represented by a borderline. On the other hand, a "contour" is a borderline of a form. Hence, a contour is more than a borderline. In speaking of a contour, one is talking about the surface on one side of the borderline whose shape the contour represents.

Consider the examples in Figure 6. If the curved line in Figure 6A is meant to be a contour it could be to represent a part of a convex shape (Figure 6B) or a concave shape (Figure 6C). Without identifying a surface to be represented, the line should not be called a "contour". In Figure 6D, the borderline (dashed line) indicates the contour of the square. In Figure 6E, the exact same dashed line is not perceived as the contour of the central square area. It is perceived as a collection of parts of contours from the surrounding objects. Now, consider illusory contours. The illusory "contours" perceived in Figures 1

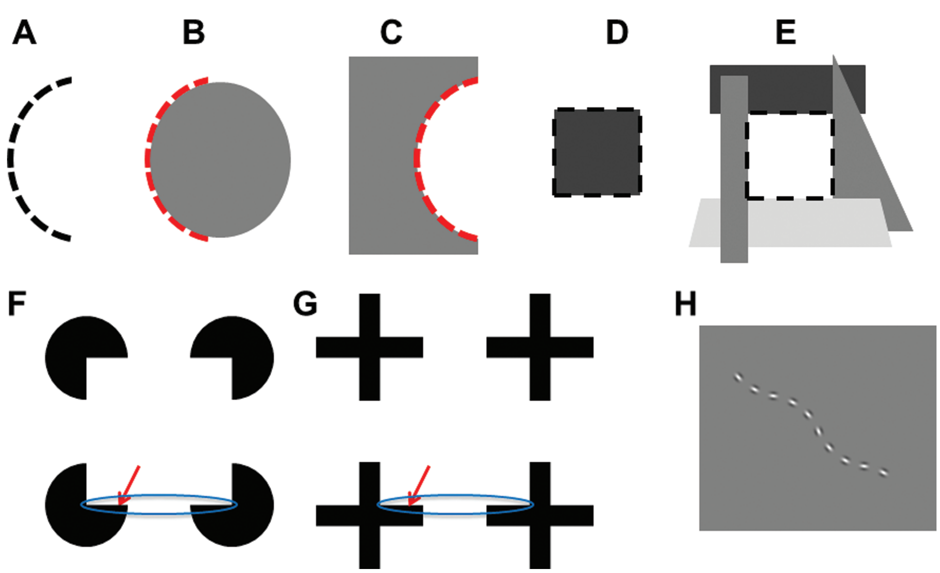

Figure 6. A to C: If a borderline is drawn as in A, it could be a part of a contour of a convex shape as in B or a concave shape as in C. The line in A itself does not carry the information in terms of which surface it represents. D: The borderline (dashed line) represents the contour of the square. E: In this case, the identical borderline as in D does not represent a contour of one particular figure. F: Kanizsa image. The straight part of the boundary (red arrow) is a part of the contour of the central illusory surface. G: Non-illusory variation of the Kanizsa image. The straight part of the boundary (red arrow) is a part of the contour of the cross object. In both F and G, the straight boundaries with the same size (blue ovals) are aligned in the same way. H: A typical "snake" image commonly used to investigate the "contour integration" mechanism. But is this really a contour?

and 2A, for example, are indeed contours because they are accompanied with (and they define the shape of) illusory surfaces enclosed by them. This is an essential observation. When comparing the images in Figure 2A and Figure 2B, pay close attention to the straight part of the boundary in the surrounding objects (Figure 6F and 6G, red arrows). In Figure 6F, it is a part of the edge of the central (illusory) surface, whereas in Figure 6G it is a part of the edge of the cross object. This already implies that, for the creation of the illusory contour, the side of the contour on which the represented surface resides is of crucial importance.

A contour is a borderline representing a form. Hence, a borderline is qualified as a contour only if it indicates a surface. Hence, the usage of the term "contour" inevitably implies that a surface on one side of a boundary is to be described. The *side matters*. This is an essential property of the concept of "contour", which clearly distinguishes it from the concept of "borderline". However, the fact that the side has to be specified when speaking of contours is often ignored in perception research. For example, a line such as Figure 6A has often been called a contour without specifying the side of the surface it represents. This confusion probably stems from our daily practice of line-drawings. When we draw a line, it could be a line-like object, a borderline, or a contour and it totally depends on what we mean to draw. The meaning of the line is not determined by the intrinsic properties of the drawing itself. Only when one draws a line meaning to represent a surface, the line is a contour. For example, when a line is drawn forming a circle, it could be a circular borderline to separate the inner area and the outer area, or a ring as an object, or a contour of a disc. However, this non-intrinsic nature of the meaning of line-drawings is often forgotten and all line-drawings are treated as contours.

Typical examples of this confusion are found in research applying so-called "snake detection" in relation to association field theory (Field, Hayes, & Hess, 1993). In this research tradition, images with co-curvilinearly-aligned Gabor patches (forming a "snake") are used (Figure 6H). Grouping the elements forming a "snake" is considered to indicate a so-called "contour integration mechanism". However, a "snake" is not a contour. If it is called a snake it is an object at best, but usually it is a simple curvilinear arrangement of oriented elements, not more than that. Even if it is meant to be a borderline (as a representation of a boundary), it does not represent the shape of a surface on one of the two sides of it and therefore it cannot be a contour. Furthermore, a contour is a *representation* of a surface. If the research is about how the edges of surfaces are detected and processed in visual cortex, it is quite odd to use *the representation of* a surface, a contour line-drawing, instead of the surface itself for experimental purposes. (See also our commentary paper (Kogo & Wagemans, 2011) on Watt and Dakin (2010).)

As such, a line as an object, a line as a borderline and a line as a contour are used interchangeably and their concepts are often confused in perception research. This is the origin of the problem. A borderline should be called a contour only when the boundary is an edge of the surface. If the surface of interest is not given or defined, its "contour" is not either.

In the next section, we explain that what is missing in the "line-drawing approach" is the fact that the completion is a phenomenon associated with a creation of surfaces. In creating surfaces, the relationship among the depth of surfaces (being occluded or occluding others) must be determined, which, importantly, requires a consideration of the global configuration of a given image. Completion may be the result of a process to construct surfaces, which is tightly coupled with computation of depth orders as an *emergent property*.

Border-ownership and its computation as an emergent property

In the preceding sections, we have argued that the completion mechanisms seem to be tuned to the construction of surfaces; hence, the side of a boundary on which the surface exists is essential to the process. We have also argued that the term "borderline" lacks the quality needed to describe a surface on one particular side of the borderline, whereas the term "contour" is meant to represent the shape of one of the surfaces. If a contour is to indicate the shape of a surface, the contour signals must be assigned to the side to which they belong. This quality of signals has been called "edge assignment" or "border-ownership".

The concept of border-ownership (BOWN) is especially important when the computation of depth order is considered (Figure 7). If an image such as that shown in Figure 7A is presented, our interpretation is that the central rectangle is on top of the background. This interpretation can be visualized as shown in Figure 7B. The borderline, then, represents the edge of the rectangle. In that case, it is said that the borderline is "owned" by the rectangle. Note that, at each location on a boundary, there are two possible ownerships (Figure 7C bottom). At some point, the competition is resolved and one side wins the ownership.

"Border-ownership" is a subjective aspect of our perception, it is not a physically defined intrinsic

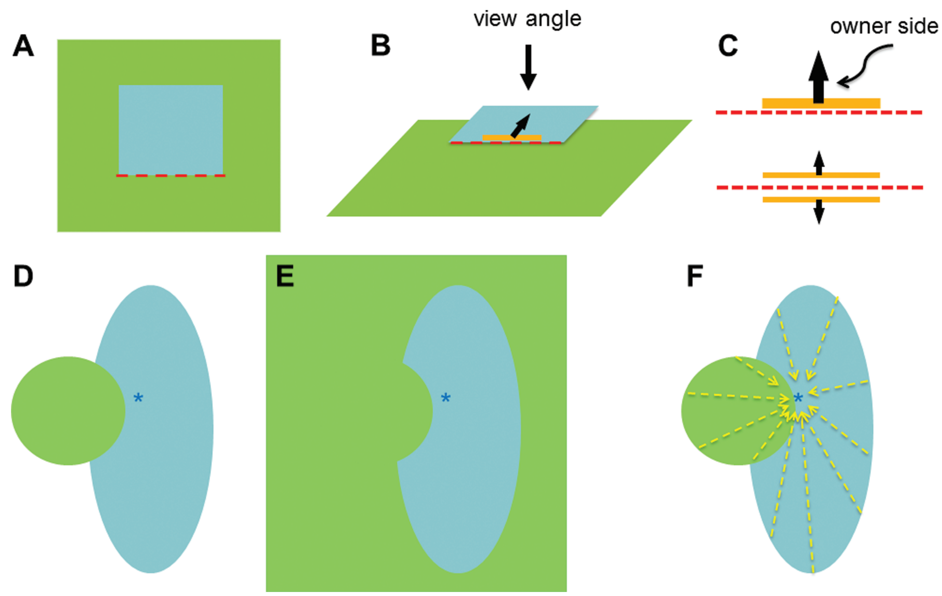

Figure 7. BOWN signal and its emergent or Gestalt property. If an image as in A is shown, it is interpreted as in B, which means that the borderline marked by the red dashed line is "owned" by the blue surface. C: In this paper, a BOWN signal is indicated by the symbol shown on top, a line parallel to the borderline with an arrow indicating the side of the owner surface. D and E: The same borderline (*) can be owned by the green disc (D) or by the green surface (E) and hence BOWN is influenced by the global configuration (F).

property of the image. It is a macroscopic property reflecting the global configuration of the image and its interpretation. In an image such as that shown in Figure 7D, a green disk on top of a blue oval is perceived. In that case, the part of the borderline between them (indicated by an asterisk) is "owned" by the green disk. If the image is now the one shown in Figure 7E, though, the blue object is perceived as a figure on top of the green background. The ownership of the same part of the borderline (asterisk) now reverts to the side of the blue surface. However, the part of the borderline marked by an asterisk in Figure 7E does not differ from the one in Figure 7D. What is different is the rest of the image. Therefore, the ownership reflects the global configuration of the image. This property of BOWN signals clearly differs from borderline signals, which merely reflect the contrast of local properties. The fact that BOWN perception is dependent on the global configuration means that it is an emergent or Gestalt property, and local properties (and the simple sum of them) cannot explain BOWN perception.

Importantly, Zhou, Friedman, and von der Heydt (2000) showed that the neural responses in V1, V2 and V4 correspond with the perception of BOWN, reflecting the macroscopic properties of the image outside of the classic receptive field. This gives a great advantage in investigating BOWN computation, which may shed light on the underlying mechanisms of the emergent properties in our perception. It is of key importance to find out how neurons achieve this context-sensitive mechanism in computing BOWN and figure-ground organization. Some of the computational models that compute BOWN (Craft, Schutze, Niebur, & von der Heydt, 2007; Froyen, Feldman, & Singh, 2010; Jehee, Lamme, & Roelfsema, 2007; Kogo, Strecha, et al., 2010; Thielscher & Neumann, 2008; Zhaoping, 2005) have something in common: BOWN signals are enhanced when there are other BOWN signals that are in agreement in terms of the ownership side, and this interaction can happen between signals at a long distance (see also the pioneering studies by Kienker, Sejnowski, Hinton, & Schumacher, 1986, and Vecera & O'Reilly, 1998, in which top-down signals bias the BOWN computation to determine the figure-ground organization). The grouping must be done based on the agreement of the owner side. Expanding this global interaction mechanism, our model explains illusory contour perception, as discussed in the next section.

The global interaction and the concept of "free-space BOWN"

Nakayama et al. (1989) argued that the classification of "intrinsic" and "extrinsic" contours is the key to explaining completion. Intrinsic contours belong to the surface of interest while extrinsic contours are the accidental consequence of occluding surfaces. Hence, the shapes of the completed surfaces are perceived only after establishing the depth order of surfaces and detaching them from the extrinsic contours. This classification of contours corresponds to the computation of BOWN. In line with this view, we argue that our perception of illusory contours in Kanizsa-type images corresponds to activations of BOWN-sensitive neurons at that location as the result of the BOWN computation by the global interactions.

The aforementioned models to compute BOWN (Craft et al., 2007; Froyen et al., 2010; Jehee et al., 2007; Kienker et al., 1986; Kogo, Strecha, et al., 2010; Thielscher & Neumann, 2008; Vecera & O'Reilly, 1998; Zhaoping, 2005) are made to reflect the global configurations of the image. The global interactions can be applied further to create illusory contours. In essence, this is the approach taken by some of the models (Finkel & Sajda, 1992; Geiger, Pao, & Rubin, 1998; Kogo, Strecha et al., 2010; Sajda & Finkel, 1992; Williams & Hanson, 1996). In our model, called the "Differentiation-Integration for Surface Completion" or DISC model (Kogo, Strecha et al., 2010), the logic behind the implementation is quite simple. As BOWN is a global property, the BOWN computation in the model allows all elements in the entire image to interact globally with one another (Figure 7F). First, it is assumed that the BOWN-sensitive neurons (Zhou et al., 2000) are distributed in retinotopic space to cover the whole visual field (Figure 8Aa). The preferred locations and orientations of some of these neurons may correspond to the locations and orientations of the boundaries in the given image. If, in addition, their preferred owner side corresponds to the owner side determined by the BOWN computation process, these neurons would be active (Figure 8Ab). Importantly, the other neurons that are *not* located at any of the given boundaries may not receive direct activation from the image but, as a result of the BOWN computation with the global interactions, they may also be activated by some specific configural aspects of images such as the Kanizsa figure (Figure 8Ac). These signals of the BOWN-sensitive neurons that are *not* located at given boundaries are called "free-space" BOWN. The global interaction of BOWN signals is based on the consistency of the owner side decided by the geometrical relationship between them, as shown in Figure 8B. This interaction works in favor of convex shapes (Figure 8C).

With this approach, the model is able to distinguish the illusory and non-illusory images in their BOWN maps (Figure 9). The key is the difference of the BOWN signals at the straight boundaries that surround the central square area in the two images (Figure 9A). First, at each location on the boundaries, two competing BOWN signals are assumed with the opposite preferred owner side. Each BOWN signal computed at a location (e.g., Figure 9B, blue disks) is influenced by all other BOWN signals, based on the "consistency of owner side" rule mentioned above. When applying this algorithm iteratively, more final BOWN signals are obtained in the following way (Figure 9C). Considering the pacmen in the illusory figure (Figure 9C, left), the straight part of the boundary is owned by the central area, while the curved boundary is owned by the pacmen. This indicates that there is an occluding surface in the central area on top of the surrounding objects, creating the "illusory T junctions" on the side corners of the pacmen. For the crosses in the non-illusory figure (Figure 9C, right), on the other hand, all boundaries are owned by the crosses, i.e., the crosses are perceived as individual objects which are fully visible and bounded by intrinsic contours. Next, based on these BOWN signals and assuming the free-space BOWN signals, the global interaction is repeated at each location in the entire space (e.g., at the location where an illusory contour may be perceived, Figure 9D). As a result, illusory BOWN signals develop in the illusory figure (Figure 9E) but not in the non-illusory figure (Figure 9F). The neural activities at the locations where the illusory contours are perceived (von der Heydt et al., 1984) correspond to this configurality-dependent activation of free-space BOWN-sensitive neurons. In other words, although physically existing boundaries may be detected at an early stage of the visual cortex and their ownerships may be computed later, the creation of illusory contours in the Kanizsa figure may work differently: BOWN signals at the locations of illusory contours could be created by directly activating the BOWN signals without the preceding creation of boundary signals.

In fact, Heider, Spillmann, and Peterhans (2002) showed that neurons that are activated at the location of illusory contours created by stereo images are sensitive to the polarity of the depth difference. These neurons are very likely the BOWN-sensitive neurons and hence in agreement with our hypothesis. Many models that reproduce modal completion in the Kanizsa figures (i.e., by creating "illusory contours"), however, start from the completion of the gaps based on the collinear alignment. The BCS/FCS systems theory (Grossberg & Mingolla, 1985a, 1985b) and its successor, the FACADE theory (Grossberg, 1994), have strongly developed since the original publication, and they have been shown to yield robust responses to various test images. However, no matter how much the theory has progressed, the foundation of the theory is still the concept of so-called "bipole cells" that detect and

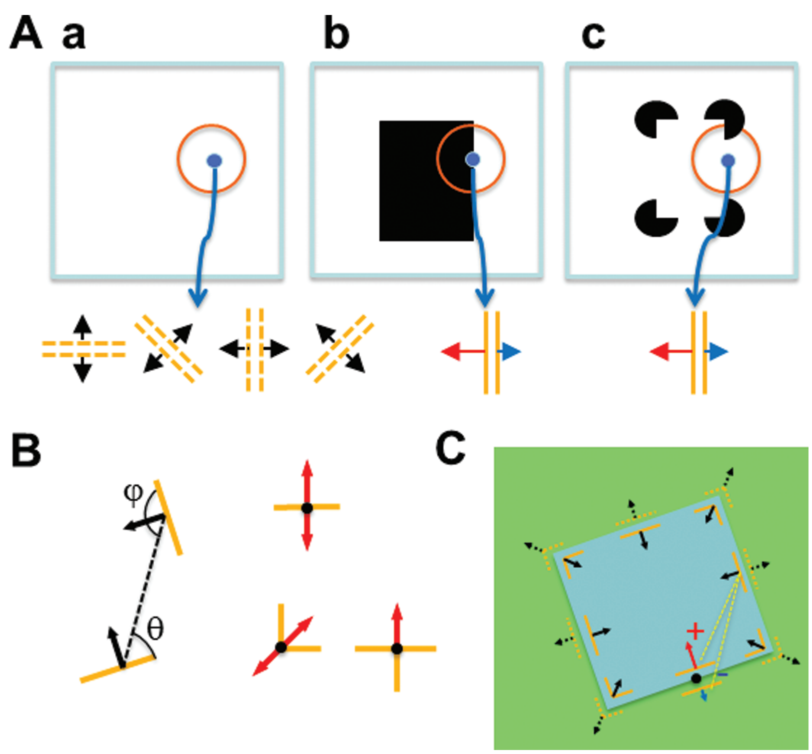

Figure 8. A: The concept of "free-space BOWN". In the visual field (blue square) it is assumed that the BOWN-sensitive neurons with different preferred orientations and preferred owner sides are equally distributed (e.g., at the location indicated by the blue dot) (a). When an image such as a rectangle is given, a particular BOWN-sensitive neurons are activated (red arrow) and the competing signals (blue arrow) are inhibited by the neural circuit made for global interactions (b). Even when BOWN-sensitive neurons do not correspond to the location of the edges of the figure, they may be activated by a figure with specific configurations such as Kanizsa figure, as a result of the global interactions (c). B: The global interaction implemented in DISC model is based on the consistency of the owner side. For example, when two BOWN signals on boundary elements fulfill the condition of "agreement", $0° <= \theta < 180°$ and $0° <= \varphi < 180°$, they are enhanced and, when they do not, inhibited (left). BOWN signals are given to all boundary elements and L- and T-junctions at first (with two competing signals for boundary elements and L-junctions, and a signal of ownership above the top for T-junctions) (right). C: The interaction is made for all possible combinations of boundary elements in the image. This algorithm works in favor of convex shapes.

complete the collinearly aligned boundaries. A recent model by Thielscher and Neumann (2008) does compute the border-ownership (edge assignment) of the Kanizsa figure. However, even in their model, the illusory borderlines are first created by the bipole cells and the BOWN computation is only then derived from that. In other words, it is assumed in their model that the completion is done before the BOWN is computed. The model proposed by Heitger et al. (Heitger, von der Heydt, Peterhans, Rosenthaler, & Kübler, 1998; Peterhans & Heitger, 2001) reflects the difference polarity of end-stopped signals and hence the side of the occluding surface. These signals are grouped by so-called grouping operators similar to the bipole cell in the model by Grossberg and Mingolla (1985a, 1985b). Therefore, this model reflects the side of the ownership based on the local cues but the grouping of the collective signals are based on their collinear alignment of the signals. It is not clear whether this approach can reflect the context-dependent difference between the illusory and non-illusory figures. In contrast, the models that reflect the global configurality in their computations reproduce the context-sensitive properties of completion (Finkel & Sajda, 1992; Geiger, Pao, & Rubin, 1998; Kogo, Strecha et al., 2010; Sajda & Finkel, 1992; Williams & Hanson, 1996). This indicates that the computation of the side of the illusory surfaces by reflecting the global configuration is fundamental in the completion process.

The activation of the illusory contour signals should not be considered as a "line-drawing" process at the gap. It corresponds to the activation of BOWN signals, which therefore indicate more than just the location of the boundary. The computed BOWN signals indicate which side of a borderline is the owner side and, hence, is closer to the viewer than the other side. In other words, the BOWN signals indicate the *polarity* of the difference in depth by indicating the side of the figural surface. This is fundamentally different from borderline signals that merely indicate the existence of a

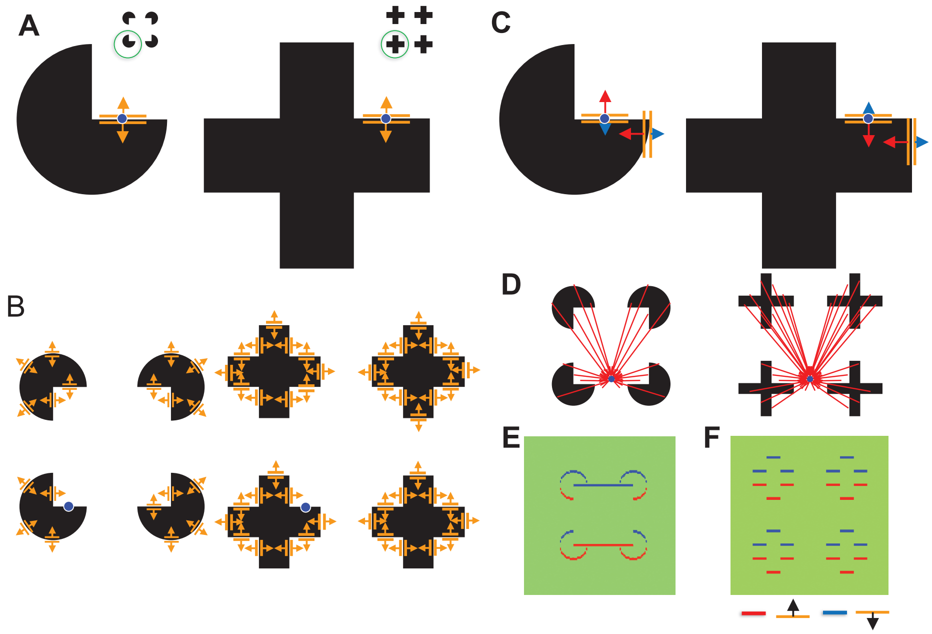

Figure 9. The difference of BOWN signals in illusory and non-illusory figures as the result of global interactions. A: At first, two competing BOWN signals with opposite preferred owner side are assumed. Examples of the initial BOWN signals at a location of the straight boundary of a pacman (left) and the corresponding part in the cross object from the non-illusory figure (right) are shown. B: The global interaction algorithm is iterated to compute the BOWN signals at each location of the boundaries. C: The computer simulation of the interaction creates different BOWN signals along the boundaries of the surrounding objects in the illusory (left) and the non-illusory (right) figures. In the non-illusory figure, the BOWN signals in the cross object consistently indicate the ownership by the object. In the illusory figure, the BOWN signals are not consistent around the side corner of the pacman, the condition suggesting a possible (illusory) T-junction. D: Further global interactions are made including the free-space BOWN signals in the entire space. E, F: BOWN maps in the Kanizsa figure (E) and the non-illusory figure (F). The difference of the competing BOWN signals for the boundary of horizontal orientation are shown. The owner side is the upper side when the signal is red and it is the lower side when the signal is blue. In E, the gap between the aligned straight boundaries is filled-in with BOWN signals (the central square as the owner), while it is not in F.

difference but not its polarity. For a neurocomputational account, this difference is significant. To indicate a borderline, only one signal at each point at the boundary needs to be present. In contrast, to indicate the polarity, two opposite neural signals at each point at the boundary are necessary. This quality of BOWN signals carrying the polarity of a difference is similar to differentiated signals in mathematics. Differentiated signals not only show the absolute values of differences but also preserve the signs of differences (increase or decrease in a predefined direction) and, because of this quality, 2-D spatial integration can reproduce the original signals. Hence, BOWN signals can be considered as two-dimensionally distributed differentiated signals in the depth domain. Importantly, although BOWN concerns information in the depth domain, this view can be generalized. It is possible that the visual cortex is designed to construct differentiated signals in various domains (lightness, depth, texture, etc.) at an early stage, and surface signals are constructed from them later at a higher level (e.g., Retinex theory for modeling the lightness perception; Land & McCann, 1971). We have called this the "differentiation-integration" approach. The paradox that Hubel pointed out (see Problems: Inconsistencies in the " line-drawing" approach section) is due to the fact that, by recognizing the neural activities as borderline signals, the implicit information about surfaces is ignored. If the neural activities at the lower level of visual cortex are considered as differentiated signals, surfaces (the "interior") are indeed signaled in the visual system as implicit information, which then becomes explicit at the higher level with the surface construction process.

Furthermore, it is possible that the very fact that "differences" of certain values are detected first in the visual system is the origin of the "relational" properties of our perception. As Gestalt psychologists argued (Koffka, 1935), our perception often ignores absolute values of input signals and only detects relationships between the signals (e.g., in identifying a melody with various pitches, the relationship between the notes in the sequence, rather than the absolute values of those notes, is the important feature). In fact, the DISC model is able to reproduce such relational properties and the anchoring phenomenon in lightness perception (Kogo, Van Gool, & Wagemans, 2010).

In summary, BOWN signals are constructed as a differentiated form of depth signals and their integration creates surfaces with a given depth order. The computation of BOWN signals must reflect the global configuration of the image. It is possible that the illusory contours perceived in Kanizsa-type images correspond to the BOWN signals resulting from global computation (free-space BOWN activation). This can explain the context-sensitivity of the Kanizsa illusion.

IMPLICATIONS: HOW IS COMPLETION LINKED TO NEURAL ACTIVITIES?

We began this paper with the contention that it is important to determine the real meaning of the neural activities at the location of illusory contours (von der Heydt et al., 1984). We explained how the polarity of differences should be preserved in neural activities and that BOWN computation, which reflects the global configuration of images, is essential to explain the emergence of illusory contours. In this section, we discuss the implication of this view for interpreting the response properties of neurons in visual cortex.

Von der Heydt et al. (1984) showed that when a stimulus that evokes an illusory contour whose location and orientation match those of the classic receptive field, many neurons in V2 showed an increase of their activities as if they were responding to existing contours. This result has often been interpreted as evidence of neurons filling-in the gap of aligned contours, referred to as "borderline completion" in this paper. However, to determine if this neural "completion" response truly corresponds to the perception of illusory contours, it is necessary to compare the neural responses in the Kanizsa figure and in the non-illusory figure. If the neurons show responses at the gap, regardless of whether the figure is illusory or non-illusory, the neural activities do not correspond to our perception of illusory contours and factors such as collinear alignment are sufficient to explain this activation. In contrast, responses occurring only in the illusory figures but not in the non-illusory figures would strongly suggest that these neural activities are crucial for the emergence of completion. Indeed, some reports indicated that these neurons did not show responses or showed only weaker responses to non-illusory figures (Grosof et al., 1993; Lee & Nguyen, 2001; Peterhans & von der Heydt, 1989; von der Heydt & Peterhans, 1989b; von der Heydt et al., 1984). Some neuroimaging and EEG studies also showed a difference of brain activities in response to illusory and non-illusory figures (Ffytche & Zeki, 1996; Goebel, Khorram-Sefat, Muckli, Hacker, & Singer, 1998; Halgren, Mendola, Chong, & Dale, 2003; Herrmann & Bosch, 2001; Hirsch et al., 1995; Kruggel, Herrmann, Wiggins, & von Cramon, 2001; Larsson et al., 1999; Mendola, Dale, Fischl, Liu, & Tootell, 1999; Murray et al., 2002; Proverbio & Zani, 2002; Ritzl et al., 2003; Seghier et al., 2000; Stanley & Rubin, 2003; for a review, see Seghier & Vuilleumier, 2006). Therefore, it is very likely that the neural circuits responsible for illusory contour perception are context-sensitive and reflect the global configuration of the images. However, none of these studies incorporated both of the following conditions simultaneously: (1) Both the Kanizsa figure and its non-illusory variations are used and (2) the non-illusory figures have collinearly aligned borderline segments that have exactly the same length and distance as the illusory figure (Figure 2A and 2B). As discussed in this paper, it is important to investigate if the neural activities reflect the contextual differences between Figure 2A and 2B.

The most important assumption in our theory is that the neurons that show activities corresponding to illusory contours in the Kanizsa figure are BOWN-sensitive neurons (we call these signals "free-space" BOWNs). Although the BOWN-sensitive neurons have also been shown by von der Heydt's group (Zhou et al., 2000), it has not been determined whether the illusory contour-sensitive neurons belong to this class as well. However, empirical data indicate that some neurons active at illusory contours reflect figure-ground organization (Baumann, van der Zwan, & Peterhans, 1997) and are sensitive to depth differences defined by stereo disparities (Bakin, Nakayama, & Gilbert, 2000; Heider et al., 2002). If the neurons active at the illusory contours in the Kanizsa figure are indeed BOWN-sensitive neurons, it would make a strong case against the "line-drawing" point of view because (1) BOWN signals do not merely indicate the existence of a depth difference, but also indicate the polarity of the difference and (2) BOWN signals reflect the global configuration of an image. It would also make a strong case for the involvement of depth-order computation in creating illusory contours (Anderson & Julesz, 1995; Coren, 1972; He & Nakayama, 1992; Nakayama et al., 1995; Nakayama & Shimojo, 1990, 1992; Nakayama et al., 1989; Tse, 1999a, 1999b).

Furthermore, an important property of BOWN perception has been reported. On the one hand, it has been shown that activities of BOWN-sensitive neurons are influenced by attention (Qiu, Sugihara, & von der Heydt, 2007), which is further supported by human brain imaging (Fang, Boyaci, & Kersten, 2009). On the other hand, there is psychophysical evidence indicating that attention (Peterson & Gibson, 1991) and context, such as the familiarity of the shapes of the figures (Peterson & Gibson, 1994; Peterson, Harvey, & Weidenbacher, 1991), can influence the alternation of figure-ground perception in face-or-vase type images. Importantly, a thorough analysis of the temporal properties of the neural activities reported in the series of papers by von der Heydt's laboratory indicates that the very fast signal processing in the BOWN computation can be done only by the feedforward-feedback loops not by the horizontal connections (Craft et al., 2007; Sugihara, Qiu, & von der Heydt, 2011; Zhang & von der Heydt, 2010; Zhou et al., 2000).

These results suggest two important views on BOWN computation. One is the existence of a dynamic feedback system between the lower level and the higher level neural activities. If the higher level visual cortex constructs a depth map of an image (as in the DISC model), and projects signals back to the lower level BOWN-sensitive neurons, it is possible that this feedback system enhances the BOWN signals that are in agreement with the detected depth order at the higher level and suppresses the signals in disagreement, further emphasizing the emerging figure-ground perception. The second view of importance is the possibility that, when presented with an image such as a face-or-vase image, some BOWN-sensitive neurons may (or may not) show fluctuations of activities corresponding to the bi-stable figure-ground perception (Kogo, Galli, & Wagemans, 2011). Alternatively, it is also possible that the figure-ground organization determined at the higher level deviates from what is signaled as BOWN at the lower level, and that the BOWN-sensitive activities in the lower level visual cortex do not always correspond to our perception. The neural evidence for a feedback influence on BOWN-sensitive activities (Fang et al., 2009; Qiu et al., 2007) and the psychophysical evidence for a feedback influence on multi-stable perception (Peterson & Gibson, 1991) suggest the former case. In fact, MEG recording combined with the frequency tagging method showed bi-stable activities corresponding to human subjects seeing face-or-vase in the early stage of visual cortex (Parkkonen, Andersson, Hämäläinen, & Hari, 2008).

The systematic investigation of BOWN-sensitive neurons with neurophysiological recordings in the hierarchy of the visual cortex in relationship to illusory contours, figure-ground organization, multi-stable perception and feedback, would provide vital information regarding the dynamics of the neural signal processing, which determines the perception of figure-ground organization and the depth order of images, including ones with illusory surfaces.

CLOSING REMARKS

In this paper, we critically discussed the conventional view of "contour-completion" as an underlying mechanism. We pointed out the problems with the "line-drawing" point of view and confusion regarding the definitions of the terms. To reproduce the completion phenomenon properly, the concept of "border-ownership" (BOWN) is essential, and the global configuration of the images must be reflected in order to compute BOWN. Signal processing proceeds two-dimensionally to (re-)construct surfaces. Line-wise grouping is not what the visual system is evolved to do. Although neurons in early visual cortex may appear as "borderline detectors", some of their signals implicitly carry the 2-D information by preserving the polarity of difference. The side matters. This is the reason why the completion in the Kanizsa figure corresponds to the development of the illusory surface in the center. The combination of the BOWN computation and the differentiation-integration approach implemented in the DISC model (Kogo, Strecha et al., 2010) realizes this view by first reflecting the 2-D configuration of the image into BOWN signals and then spatially integrating them to construct surfaces. We further suggested that the perception of illusory contours corresponds to the activation of BOWN-sensitive neurons in early visual cortex that are activated not directly by the input but by the effect of global interactions in the BOWN computation (free-space BOWN).

This aspect of BOWN computation by global interaction is a prototypical case to support the crucial importance of perceptual organization in vision. How, in neuro-mechanistic terms, does the so-called global property of our perception emerge? This property of BOWN cannot be explained by simple summation of local properties but corresponds to the concept of "configurality" or "context". In other words, it is an emergent or Gestalt property. Understanding how the global configurality or context is reflected in computations that produce the emergent properties of human perception is a rather challenging goal. We consider it one of the most important research questions, not only in vision science but a wide range of other research fields, from computer vision to philosophy. The attempt to compute BOWN signals that correspond to our perception (including the illusory BOWN) is a first step to achieve such a goal. Further investigation is needed to understand the underlying neural mechanisms to create this Gestalt property of our perception. We believe that the views provided in this paper along with the suggested neurophysiological investigations contribute to such an understanding.

Original manuscript received 13 December 2011
Revised manuscript accepted 22 August 2012
First published online 5 October 2012

Commentaries

Long range grouping mechanisms for object perception

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http://dx.doi.org/10.1080/17588928.2012.748021

Abstract: The case made by Kogo and Wagemans for border ownership of surface boundaries to explain modal completion of illusory contours is well argued, and is compatible with psychophysical and physiological research on configural interactions with stereoscopic depth processing. However, it is important to contextualize such a mechanism of surface interpolation with related object grouping mechanisms in visual cortex, such as those not necessarily related to depth. Additionally, it's worth considering how the BOWN model can be generalized beyond Kanizsa shapes to more complex volumetric surface interpolations.

The modally completed contours of the Kanizsa square is one of the most engaging illusions of visual science, and Kogo and Wagemans' emphasis on configural aspects such as border ownership (BOWN) for its perception is important. It seems to us that the combination of local and global computations in visual cortex is crucial for contour interpolation, and helps to explain the need for multiple retinotopic visual areas in the brain with increasing receptive field size. The authors' model is compatible with data from physiological recording studies, such as the work of Von der Heydt and colleagues (e.g., Zhou, Friedman, & von der Heydt, 2000), yet the precise mapping of the full network involved is not yet clear. The additional complexity of representing three-dimensional depth may well share similar mechanisms, but questions still remain.

We have previously noted the formal similarity between images that encourage long-range grouping of image elements, but may or may not have implied depth (Mendola, 2003). For example, Tyler et al. (2005) showed that random dot patterns with a vertical axis of symmetry compared to random dot patterns without symmetry produce fMRI activation patterns that resemble those obtained by contrasting aligned versus misaligned Kanizsa inducers. Specifically, the higher-tier areas in the lateral occipital cortex are activated by both comparisons, and we suspect that long-range global grouping mechanisms such as those discussed by the authors for BOWN might be located in these cortical regions.

On the other hand, unlike symmetrical dot patterns, the Kanizsa shape produces a figure that owns its borders and segments from the background. We expect that those modally completed borders are precisely represented by (BOWN) neurons in lower-tier areas such as V2 or V1, and we consider feedback from higher- to lower-tier areas the likely mechanism (Rabbel, Dale, Mendola, & Halgren, 2000). Is such a feedback-related BOWN signal the main difference between representations of these two image classes? Is there differential recruitment of lateral connections within area, or areas that code 3D depth explicitly? Yet a third class of images is the traditional "contour integration" Gabor-array patterns, called "snakes" by Kogo and Wagemans. Without cues to closure, such images may lie in the middle of a continuum with regard to implied depth, but the snakes do invoke minimal figure ground segmentation. Future experiments are needed to clarify how the neural substrates differ across these classes.

Another line of relevant experimentation involves the interactions between multiple cues to depth. A now classic paper by Gregory and Harris (1974) shows that when stereoscopic depth information inconsistent with the typical border ownership of a Kanizsa shape is presented, the illusory contours are less visible or disappear entirely. In rare cases of cue conflict subjects even reported illusory shapes curved in depth. Recent physiological support for single neuron overlap between the processing of border ownership and stereoscopic depth contours (Qiu & von der Heydt, 2005), supports this interaction and argues for a model that can integrate such cues.

Kogo and Wagemans rightly envision the inference of BOWN as necessary to calculate the order of separable objects in depth. However, it should be emphasized that, when considering images outside of simple two-dimensional shapes—particularly self-occluding objects like those presented by Peter Tse (1999)—BOWN

The authors are supported by an NSERC Discovery Grant and a LOF award from CFI.

cannot simply be understood as contour side-dependent. Rather, the individual surface components of the object are side-dependent, and any perception of border or volume ownership results from further contextual processing. Although the BOWN model presented here is well-suited to interpolate figural contours from a Kanizsa square, we hope that the model is robust enough to work for unconventional or complex 3D images as well. It is our speculation that such robustness in the human visual system results from the high degree of cross-modal redundancy present for surface signals in natural viewing conditions. This covariance across cue modalities likely contributes to top-down constraints on lower-level featural processing, and eventually allows for surface interpolation even in "impoverished" images such as the Kanizsa square.

* * *

"Connectability" matters too: Completion theories need to be complete

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http://dx.doi.org/10.1080/17588928.2012.748022

Abstract: Kogo and Wagemans provide an intriguing way of assigning a polarity value to closed edges in fragmented images (solving the border ownership problem), but their model lacks generality and disregards connectability as a relevant aspect of visual completion. The lack of generality depends on considering concave disk sectors (pacmen) as the main inducers of illusory contours. Connectability is crucial for defining the occurrence, the salience and the shape of completed contours. A complete theory of completion should integrate border ownership and connectability, rather than emphasizing one aspect over the other.

Kogo and Wagemans (this issue, K&W) take a bold position against models of illusory contours based on line interpolation; i.e., on the notion that essential aspects of such perceived entities depend on processes that fill gaps between line segments included in an intermediate representation in which surface information has been lost. Though sympathetic with such a view, we think that the K&W paper (1) does not clarify if the DISC model aims at accounting for all aspects of all types of illusory contours; and (2) underestimates the importance of connectability as a constraint for illusory contour formation.

Generality

The K&W model captures important aspects of contour segmentation and surface completion processes originally invoked by Kanizsa (1955), with reference to the effectiveness of concave disk sectors (pacmen) as inducers of illusory contours, which possibly constitute a heterogeneous set of phenomena grouped under a theoretically unfortunate label. However, the K&W model does not seem well-suited to explain illusory figures induced by convex regions (Albert, 1993), as well as by line endings, which enhance the salience of the classic Kanizsa triangle and act as the only inducers of powerful illusory contours in several configurations, including the so-called Koffka cross. More critically, the BOWN computation seems irrelevant for explaining the amazing effect of dots on shaping the illusory blob induced by line endings of the Koffka cross or similar configurations (e.g., Gerbino & Kanizsa, 1987). In such configurations, the addition of dots (by themselves only capable of defining "virtual" trajectories; Kanizsa, 1955) to line endings produces strong cooperative effects constrained by connectability along a smooth trajectory (for a critical difference between line endings and bars as inducers, see Sambin, 1987).

Connectability

The evidence that connectability along a smooth trajectory represents a crucial aspect of illusory contour formation is overwhelming and raises the venerable issue of homology-analogy evoked by the identity hypothesis (Shipley & Kellman, 1992) and, more generally, by any smoothness-based model of visual completion. Border ownership polarity and connectability refer to two independent aspects of optical indeterminacy, regarding: (1) the direction of occlusion; (2) the belongingness of parts to the same whole. Since both indeterminacies are pervasive in ecological optics, one might expect that several visual processes evolved to reduce the impact of their negative consequences. K&W appropriately link (as Kanizsa did) illusory contour and border ownership, but overshadow the relevance of connectability for visual completion. They do so, for instance, by showing that a model based on collinearity/co-curvilinearity cannot address some displays in Figure 3. However, such a model is scarcely representative of current approaches to connectability: For instance, our field model (Fantoni & Gerbino, 2003) as well as other models (e.g., Kellman & Shipley, 1991), describe the amodally completed contour of Figure 3F as a continuous monotonic trajectory smoothly joining the T-stems, consistent with human performance in probing tasks (Fantoni & Gerbino, 2002). Consider also that 3D surface interpolation follows connectability constraints similar to those operating in contour interpolation (Fantoni, Hilger, Gerbino, & Kellman, 2008). As regards Figure 3G, connectability does account for visual completion when the edge gradient is shallow (rather than not, as stated by K&W in their comment). Displays C–G in Figure 3 pose another problem for the K&W model. Since the proposed spatial integration propagates activation along straight pathways, an occluded angle should be always perceived as having a sharp vertex. This is contradicted by several empirical findings showing that the shape of interpolated angles is a smooth compromise between the sharp vertex solution and the straight connection between endpoints (e.g., Fantoni, Bertamini, & Gerbino, 2005). Finally, the DISC model seems unsuitable to explain the dependence of the precise shape of the interpolated path from variables like completion type (modal vs. amodal; Singh, 2004), occlusion symmetry (Fantoni & Gerbino, 2001), retinal gap size (Gerbino & Fantoni, 2006), and orientation (Fantoni, Sgorbissa, & Gerbino, 2001).

We think that the connectability of input fragments is a crucial aspect of various types of completed contours (modal and amodal). Collinearity (along a smooth trajectory) and distance are the main constraints of connectability, affecting not only the phenomenal salience of completion but also its occurrence. The connectability constraints embodied, for instance, in our field model (Fantoni & Gerbino, 2003) might be integrated in a model that uses the pattern of activations of BOWN sensitive neurons. However, more importantly, they should be integrated in any proposed mechanism of illusory contour formation, since they seem to affect all types of illusory contours (not only those based on pacmen).

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Filling-in the gaps in models of completion

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http://dx.doi.org/10.1080/17588928.2012.748023

Abstract: Kogo and Wagemans' appropriately link completion phenomena to figure-ground computations. I argue that this link can be strengthened by considering the ecological conditions that give rise to completion phenomena. However, despite their polemics, the model that they offer can be viewed as an elaboration of the "borderline completion plus filling-in" model they eschew. Finally, I argue that it is unclear whether their model can: (1) Explain how surface structure and/or border ownership modulate the shape of interpolated contours; or (2) give meaningful outputs for images of natural scenes that contain a variety of different edge types.

Kogo and Wagemans' main thesis is that completion phenomena involve figure-ground computations. I am sympathetic to understanding completion phenomena as forms of surface-level occlusion computations, and have previously argued against models that assert that an independent contour interpolation process underlies modal and amodal completion (Anderson, 2007a, 2007b). The plausibility of the case against a separable "contour interpolation" mechanism can be made by considering the ecological conditions that gives rise to modal completion. Modal completion occurs when an occluding surface is camouflaged by a more different surface. It is therefore almost tautological to assert that modal completion involves figure-ground computations, since it involves the resolution of occlusion relationships. The issue is not *whether* figure-ground computations are involved, but how information about occlusion is derived from images. In the context of the present paper, the main issue concerns whether completion is driven by interpolated 1D signals ("borderlines") that are subsequently filled-in, or whether (and what) surface-level attributes play a causal role in completion phenomena.

Given the rather extensive and elaborate discussion of the role of surface attributes in modulating completion, one might expect a model in which surfaces play a central role in explaining completion. But this is not really what K&W present. When viewed from a dispassionate distance, their model appears very similar to the "borderline completion plus filling-in" models that they eschew. The inputs into their model are local edge responses. The only significant difference is that they treat their edges as "signed" quantities, where the sign (or "polarity") designates the possible border-ownership assignments. The rather fanciful moniker of a "free-space BOWN" is, in this framework, just a polarity signal that has been interpolated (filled-in) from its local edge generator. Indeed, if the paper is stripped of the pedantics surrounding the proper use of the term "contour," what remains appears to be an elaboration of previous modeling efforts, supplemented with an additional term (a BOWN signal). This may, in fact, provide crucial leverage into understanding aspects of completion. Alternatively, the kind of BOWN units K&W consider as causal may be epiphenomenal, and play no role in *generating* the figure-ground relationships observed in completion phenomena. They could, e.g., be the consequence of region-based, top-down feedback. Although K&W briefly mention the possible contribution of feedback, they do not consider that feedback could essentially invert the causal flow, turning BOWN signals into outputs rather than inputs.

What might be wrong with the "line completion plus filling-in" architecture on which K&W build? One issue involves a growing body of data showing that border-ownership and/or information about surface shape can modulate the perceived shape of interpolated contours. Although K&W cite such data to motivate the importance of border ownership, they offer no explanation for these effects, and also fail to consider some particularly dramatic forms of shape change that accompany changes in border ownership (such as the "serrated edge illusion", Anderson, Singh, & Fleming, 2002). In its present form, their model simply selects one side of an edge as its most likely "owner" through a global consistency checking process. The shapes of interpolated contours are not affected by the regions to which they belong; they are still determined by the local shapes of the inducing elements that participate in the contour interpolation process. Surfaces are, once again, simply *outcomes* of interpolated edge elements, not causes. The polemics of their introduction led me to expect (and eagerly anticipate) a model in which surfaces were causal forces *shaping* completion, rather than the emergent consequence of interpolations from signed 1D (signed) edges. Perhaps such a model will be considered in the future.

Finally, one can also ask: *When* does the "side matter?" The authors have restricted their discussion to toy images in which all of the edges have some simple occlusion interpretation. But most natural scenes are filled with "edges" (itself a very slippery construct), only a small fraction of which correspond to occluding contours. Edges can be generated by variations in surface reflectance, variations in illumination, or by changes in surface pose. How does K&W's model know which edges to enter into a BOWN competition? The current form of the model would almost certainly generate a host of spurious BOWN signals when applied to natural images, so it seems unlikely that a model of this type could provide much insight into the kinds of images that our visual systems evolved to parse.

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Neurophysiological constraints on models of illusory contours

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http://dx.doi.org/10.1080/17588928.2012.748024

Abstract: Illusory contours can appear as interpolation between edges of the stimulus, as in the Kanizsa triangle, or run orthogonal to the inducing elements, as in the Ehrenstein illusion. Single-cell recordings from monkey visual cortex suggest that both are produced by the same mechanism. Neural border ownership coding, on the other hand, which shows a much larger range of context integration, might involve a different mechanism.

Kogo and Wagemans present a lucid discussion of the various models that have been proposed to explain the phenomenon of illusory contours, pointing out that models need to explain not only the illusory contours where they appear, but also why they do not appear in other situations. I agree in particular with their point that simple interpolation models fail these criteria. A demonstration that makes this immediately obvious is the Ehrenstein illusion in which radial lines induce a circular illusory contour (the four-armed version is shown in Figure 1A right). In this figure, interpolation of the lines would produce a cross rather than a circle. I wonder why Kogo and Wagemans (2010) and other authors did not test their model on this illusion. It might be thought that the pacman figure (Figure 1A left) and the Ehrenstein illusion (right) involve different mechanisms. However, the neurophysiology tells otherwise. In our study of illusory contour representation in monkey visual cortex, Esther Peterhans and I used two different types of stimuli, one in which an illusory contour is produced by abutting gratings of thin lines, and a configuration in which an illusory bar is induced by two solid shapes (Peterhans and von der Heydt, 1989; von der Heydt and Peterhans, 1989). In the latter configuration, the illusory contours are collinear interpolations of given edges, like in the pacman figure. But in the abutting gratings, the illusory contour is orthogonal to the inducing lines, like in the Ehrenstein figure. We compared both types of contour in a sample of neurons and found that the results correlated: Of 15 cells that signaled an illusory contour with the abutting grating stimulus, 9 also signaled one in the illusory bar configuration, and of 23 cells that were unresponsive to the former, 22 were also

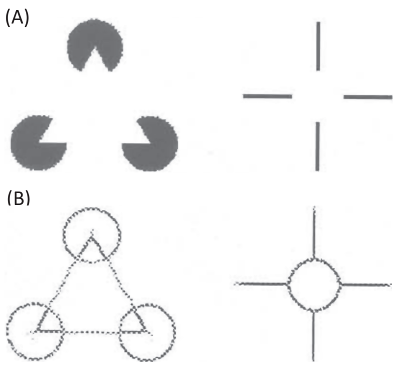

Figure 1. A, Illusory contours can appear as interpolations between edges of the inducing elements (pacman figure, left), or can be orthogonal to the inducing elements (Ehrenstein figure, right). B, Contours produced by the model of Heitger et al. 1998. Modified from Heitger et al. 1998.

unresponsive to the latter. Thus, the two tests produced correlated results ($p < 0.001$). The simplest explanation for this is that the illusory contour signals in the two situations are produced by the same mechanism. It is a challenge to produce the correct illusory contours in the pacman figure as well as the Ehrenstein figure with the same model, because one calls for interpolation, whereas the other prohibits it (see Figure 1A). To reconcile these conflicting demands was a main consideration in the model by Heitger, von der Heydt, Peterhans, Rosenthaler, and Kübler (1998), results of which are shown in Figure 1B.

Also from the neurophysiological perspective I have reservations with the claim that illusory contours and border ownership must be treated together and that the former cannot be explained without the latter, which is the main point of the review. I agree that both are related. Illusory contours reflect mechanisms for the detection of occlusion, and occlusion implies border ownership. But some findings indicate that the underlying neural mechanisms are different. Illusory contour responses, as recorded in area V2, show a limited range of context integration. Typically, these responses drop to zero when the gap between the inducing elements is wider than about 3 deg (Peterhans and von der Heydt, 1989). By comparison, border ownership selectivity, also found in V2, shows context integration over distances of 10 deg or more. Also different from illusory contours, border ownership modulation does not require "relatability" (Kellman and Shipley, 1991): Even a figure edge parallel to the edge in the receptive field contributes border ownership modulation (Zhang and von der Heydt, 2010). Together, these studies suggest that illusory contour responses might be generated by relatively local integration of signals, possibly in feed-forward fashion (e.g., Heitger et al., 1998), whereas border ownership modulation might involve feedback from a higher level (Sugihara, Qiu, & von der Heydt, 2011; Zhang and von der Heydt, 2010). Both mechanisms might contribute their shares to the strength of illusory contours as measured in perceptual studies, depending on configuration and paradigm. The wide range of context integration seen in border ownership signals and their short latencies are important constraints on modeling. Kogo and Wagemans do not discuss these constraints and how the influence of global configuration, as sketched in their Fig. 7F, can propagate so fast over large distances in cortex. This might be a problem, especially since their model uses an iterative algorithm in which signals have to travel back and forth multiple times.

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Surface reconstruction, figure-ground modulation, and border-ownership

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http://dx.doi.org/10.1080/17588928.2012.748025

Abstract: The Differentiation-Integration for Surface Completion (DISC) model aims to explain the reconstruction of visual surfaces. We find the model a valuable contribution to our understanding of figure-ground organization. We point out that, next to border-ownership, neurons in visual cortex code whether surface elements belong to a figure or the background and that this is influenced by attention. We furthermore suggest that there must be strong links between object recognition and figure-ground assignment in order to resolve the status of interior contours. Incorporation of these factors in neurocomputational models will further improve our understanding of surface reconstruction, figure-ground organization, and border-ownership.

The paper by Kogo and Wagemans (this issue) is a welcome addition to the literature on perceptual organization. The neurocomputational Differentiation-Integration for Surface Completion (DISC) model aims to explain how the visual system achieves figure-ground organization. Whereas the role of feedback and the interactions between lower and higher visual areas have often been neglected in previous models (e.g., Supèr, Romeo, & Keil, 2010; Zhaoping, 2003), the DISC model acknowledges a role for feedforward and feedback processing in surface reconstruction and points out the importance of processing over large spatial scales of the visual scene. The model is one of the few attempts to integrate depth cues, lightness perception, and border-ownership (BOWN) into a common framework for surface reconstruction (Kogo, Stretcha, Van Gool, & Wagemans, 2010). The prediction by the DISC model that BOWN and figure-ground organization can only be correctly assigned when the relative depths and positions of objects in the scene are correctly computed, is in close correspondence with our visual experience. In addition to the discussion by Kogo and Wagemans, we would like to highlight three important aspects in figure-ground organization: (1) The assignment of surface elements to a figure; (2) the role of attention; and (3) the role of object recognition and feedback processing.

The neuronal correlates of figure-ground assignment are not only evident as BOWN signals at contours but also as the enhancement of neuronal responses to image elements that are assigned to a figure. This process can be measured in a texture segregation task where a figure is segregated from a background based on a difference in the properties of texture elements, e.g., a difference in orientation (Figure 2a). When the receptive field (RF) of a neuron in the visual cortex (e.g., in primary visual cortex, area V1) overlaps with a figure, the firing rate of the neuron is higher compared to when the RF falls on the background, an effect known as figure-ground modulation (FGM), see Figure 2b (Lamme, 1995). It seems likely that the surface reconstruction proposed by the DISC model is closely related to FGM in the visual cortex. A recent study investigated the role of attention in FGM in the visual cortex of monkeys (Poort et al., 2012). If the monkeys attended a figure like the one in Figure 2a, the enhancement of neuronal responses in areas V1 and V4 evoked by the center of the figure was pronounced. However, if they directed their attention elsewhere, the response enhancement was attenuated, implying that FGM depends on the relevance of the figure for behavior. This dependence of FGM on behavioral relevance was less pronounced at the boundary between figure and background, as if the feature discontinuities that characterize boundaries are always detected, irrespective of their relevance for the task. An exciting possibility is that the processes for FGM and BOWN are coupled. The assignment of a boundary to one side might facilitate FGM on the figural side of this boundary. Conversely, the FGM signal may bias the assignment of the contours surrounding the figural surface. Furthermore, attention does not only influence FGM, but it also affects the BOWN computation (e.g., Qiu, Sugihara, & von der Heydt, 2007).

Research with simple figures (e.g., Peterson, Harvey, & Weidenbacher, 1991) and natural images (Korjoukov et al., 2012) has shown that object recognition, which depends on feedforward processing and the selectivity of neurons in higher visual cortex, is a fast process that can precede image parsing (see also Thorpe, Fize, & Marlot, 1996). Knowledge about object identity can thereby facilitate the image parsing process by feedback projections from higher, object-selective visual cortex to lower visual cortex. In other words, object recognition

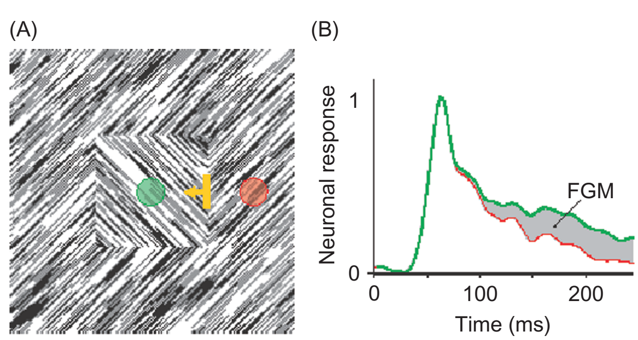

Figure 2. Texture segregation and figure-ground modulation. (a) A square figure with image elements of one orientation is segregated from a background with image elements of a different orientation. The green receptive field falls on image elements of the figure, the red receptive field on the background. Yellow arrow, border-ownership assignment of the edge to the interior of the figure. (b) Neuronal responses in area V1 evoked by elements of the figure (green) are stronger than responses evoked by the background (red curve). The difference in activity is called figure-ground modulation (gray area, FGM) (Lamme, 1995) and it is stronger for attended figures (Poort et al., 2012).

could facilitate the grouping of low level features into a coherent object representations. However, natural images often consist of different parts, i.e., they do not only have a contour which is owned by the object, but they also have inner boundaries (e.g., lines, color changes, texture lines (as in Figure 2a), etc.). Will the DISC model classify the inner boundaries of an object as belonging to separate, smaller objects or will it be able to code them as parts of a larger object? For an even better understanding of surface reconstruction, future extensions of neurocomputational models might have to also consider these inner boundaries, which could be resolved by feedback from the object recognition stage.

As a direction for further research, we suggest that it would be useful if the role of attention could be incorporated into neurocomputational models of surface completion. In addition, future models could aim to account for the perceptual grouping of various object-parts into one object, regardless of inner boundaries. We foresee that neuroimaging and neurophysiological research in combination with computational models will contribute to the better understanding of surface reconstruction, figure-ground modulation, and border-ownership and their implementation in the visual cortex.

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Borders, contours, and mechanism

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http://dx.doi.org/10.1080/17588928.2012.748026

Abstract: Kogo and Wagemans claim that subjective contours are assigned from the earliest processing stages. I argue that in making this claim, Kogo and Wagemans are mistaking subjective experience with the perceptual mechanism. There is ample evidence that before figure assignment occurs object properties on opposite sides of unassigned borders compete for perception as figures. In order for these properties to compete, these must be a point in processing at which a border exists before it is assigned to one side.

The research discussed in this commentary was supported by NSF BCS 0425650 and 0960529.

Kogo and Wagemans point out that the term "contour" should be used only when a border has been assigned to one side. This point is well taken. Both I and others have used the term "contour" for other conditions. It would increase clarity of communication in the field if we were to use it only when referring to an assigned border.

Kogo and Wagmans state that when a subjective contour is perceived, it appears to be the outer boundary of a surface or an object; that boundary assignment has already occurred. That is undoubtedly true of our subjective experience of subjective contours. In addition to making this point, Kogo and Wagemans make a more controversial claim: That an unassigned border is not present at any time in perceptual processing before a subjective contour is perceived. In other words, they argue that subjective contours are assigned from the earliest processing stages. In making this strong claim, however, Kogo and Wagemans are mistaking subjective experience with the perceptual mechanism. The fact that a subjective *contour* is perceived does not mean that there was no prior point in processing at which an unassigned border was present.

Kogo and Wagemans rightly conceive of the perception of a subjective contour as an instance of figure-ground perception in which a border between two adjoining regions is assigned to one side. The region on the side to which the border is assigned appears to be a shaped entity—the figure—and the border appears to be its bounding contour. The region on the other side seems to lack shape near the contour of the figure; it appears to simply continue behind the figure there. The current understanding of figure-ground perception is that it is the result of a cross-border competition that is affected by context (Jehee, Lamme, & Roelfsema, 2008; Peterson & Salvagio, 2008; Peterson & Skow, 2008). Kogo and Wagmans argue for competition and appeal to context effects as evidence that contours are assigned from the earliest stages of processing. My colleagues and I have proposed a different view, discussed next.

We have proposed that the properties of objects that might be perceived on opposite sides of shared borders compete for figural status. The relevant properties include image properties such as, convexity, symmetry, and closure; and subjective factors such as attention and memories of the structure of previously seen objects. We have shown that the structure of previously seen objects is assessed prior to figure assignment for a variety of border types, including subjective borders (Peterson & Gibson, 1994).

We refer to the ensembles of competing object properties on opposite sides of borders as *proto-objects* to indicate that they are considered before an object is perceived. We have presented ample evidence that inhibitory competition occurs between proto-objects on opposite sides of borders even when the final percept seems unambiguous in that the border is perceived as the contour of an object on one side only (Peterson & Enns, 2005; Peterson & Lampignano, 2003; Peterson & Skow, 2008). Moreover, we have shown that responses to the structure and location of proto-objects that lose the competition for figural status are suppressed (Peterson & Skow, 2008; Salvagio, Cacciamani, & Peterson, 2012). In order for these properties to compete, these must be a point in processing at which a border exists before it is assigned to one side.

Consistent with the view that a border is detected before it is assigned to one or the other side, Lamme and his colleagues reported neurophysiological evidence that borders are detected before figure assignment occurs (e.g., Lamme, Rodriguez, & Spekreijse, 1999; Zipser, Lamme, & Schiller, 1996). It remains a challenge to find such evidence for subjective contour perception.

CONCLUSION

The mechanism that produces the perception of a subjective contour could include an unassigned border, even if perception doesn't.

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 http://dx.doi.org/10.1080/17588928.2012.754750

Reply to Commentaries

The emergent property of border-ownership and the perception of illusory surfaces in a dynamic hierarchical system

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We argued that borderline completion does not explain the completion, that the computation of border-ownership (BOWN) causes illusory signals, and that neurons activated at illusory contours represent BOWN. Although most commentaries show support to our view, they further emphasized the importance of feedback and also pointed out some examples challenging our view. The signal processing in the hierarchy and the classification of neurons are also discussed. In this reply, we explain our position on a dynamic feedback system reflecting the global configuration, and clarify our view on completion, by examining the example figures and neurophysiological data indicated in the commentaries.

Keywords: Border-ownership; Local and global property; Illusory contours; Surface completion; Feedback; Context sensitive mechanism.

SIGNAL PROCESSING IN A FEEDBACK SYSTEM

First, it should be clear that the DISC model first detects physically given boundaries and then, based on that, it computes BOWN. However, the BOWN signals *at the location of illusory contours* are created differently. Peterson argued that, even in the case of the Kanizsa illusion, the boundaries have to be completed in the missing parts before BOWN computations. In non-illusory variations of the Kanizsa figure, if the boundaries are completed first to create the proto-objects, they need to be erased later as there are no illusory segmentations. We believe that the BOWN computation process is influenced by top-down signals in a dynamic feedback system, also in agreement with Jeurissen, Self, and Roelfsema. Our point was that the global interaction in BOWN computation creates "illusory" signals without preceding boundary completion and that this context-sensitive mechanism explains the different perception of illusory and non-illusory figures.

Peterson argued that the shapes of segmented areas are analysed individually at a higher level before figure-ground organization. We agree, and we do not believe that this view goes against our claim. First, we do not consider BOWN computation as an early stage process. BOWN computation has to reflect the global configuration and, therefore, long-range interactions between BOWN-sensitive neurons (BO neurons hereafter) are necessary. Von der Heydt's group showed that short onset latency of the BOWN component cannot be explained by horizontal connections (Craft et al., 2007). They suggested, instead, that the long-range interactions arise via feedback circuits. Although our model implements an algorithm with direct interactions between BOWN signals, we assume that in the

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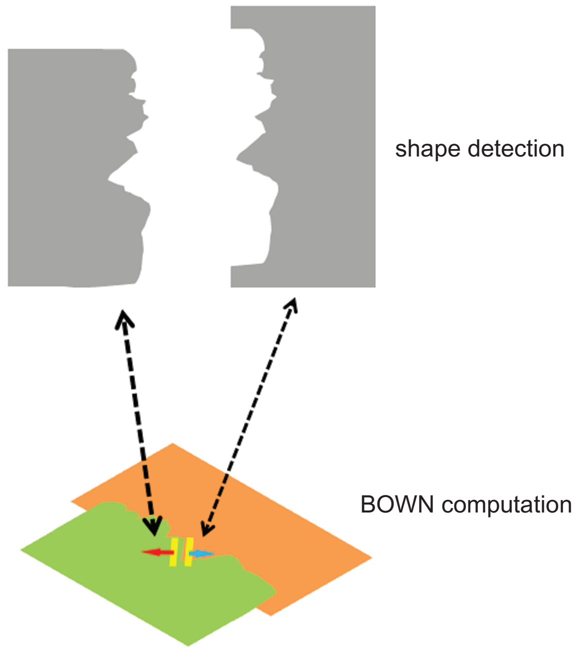

Figure 1. BOWN computation and higher level shape detection in a feedback framework. Even though the boundary between the two surfaces is owned by the left side object in our perception, it is possible that the BOWN signals on both sides are activated at first and that the action potentials are sent to the higher level for further analysis individually. Only after feedback iteration, the final BOWN (left side ownership) may be determined.

brain this is done by feedback circuits. The importance of this view is as follows: Although a hierarchically organized system may appear to complete a computation at a lower layer first and only then the computation at the higher layer starts, this is not the case in a feedback system. As shown in Figure 1, the two competing BOWN signals at a boundary of the two surfaces may be activated at first. It is possible that both signals are sent to the higher level at an early period of the computation. Only at the end of feedback interactions, the final BOWN is determined. Therefore, we are not suggesting a "figure-ground first" mechanism. BOWN is computed as a part of a dynamic feedback system.

As Anderson, and Jeurissen et al. pointed out, boundaries can be created without occlusions: Texture elements, illumination, and reflectance. Clearly, the visual system responds to various stimuli. Creating robust responses by a model is, in fact, a challenge and we agree that further development of the dynamic feedback system is important. We believe, however, that the DISC model brings in one of such context-sensitive properties, BOWN, into the computation of illusory surfaces and, hence, distinguishes itself from approaches that are based on more local properties.

ROLE OF BOWN SIGNALS IN 3D RECONSTRUCTION

One of the primary goals of vision is to respond properly to surfaces in the 3D world. Although we often use planar surfaces to investigate figure-ground organization, surfaces in the real world are commonly curved in 3D as pointed out by Mendola and Fesi ("volumetric surface"). If BOWN is about the ownership by planar surfaces only, the utility of the concept in describing the world is limited. However, we consider BOWN as a 2D differentiated signal. The edge of a planar surface is a special case where the differentiated signal indicates a step-wise change. In principle, differentiated signals can incorporate gradual as well as step-wise changes. We linked the differentiated depth map to a 2D vector field, a "gradient" (Equation 1). It is considered as an implicit description of 3D structures. It is possible that the visual system computes depth by creating differentiated signals and BO neurons constitute the bases of the vector field.

The important implication of this view is that illusory BOWN signals may not always indicate a step-wise edge of an illusory surface. In certain conditions, the edge of illusory surfaces may not appear as sharp as the ones in the Kanizsa square. The Ehrenstein figure, pointed out by von der Heydt, certainly creates salient illusory surface in the center. However, illusory surfaces may not be necessarily accompanied by step-wise edges. A surface with smooth transient edges occurs in the 3D world. While we suggest the description of a 3D profile by a gradient, we agree that the elaborated interpolation approach (Fantoni and Gerbino) may also incorporate such cases. However, it is not clear how this approach reflects context dependency of modal completion, such as the difference between the illusory and non-illusory figures. Whether the visual system conducts the boundary interpolation or BOWN-based grouping to represent illusory surfaces remains to be investigated in future research.

Anderson wrote that the algorithm in the DISC model is virtually identical to borderline-completion and filling-in. However, the differences in what is completed and how it is done are essential. Grouping boundary signals based on collinearity and grouping BOWN signals based on global configurations are two different approaches. Note that the BOWN signals on the straight edge of the pacmen indicate the ownership toward the center while the ownership of the same edges in the four crosses figure is reversed, hence reflecting the global configuration. The polarity of the signals and the reflection of the global configuration are the properties of BOWN signals that are missing in boundary signals as such. This difference is essential for future investigation of the underlying neural mechanism as there are different populations of neurons representing boundary signals and BOWN signals.

Qiu et al. (2005) reported that many BO neurons respond to stereo-disparity when it is consistent with the preferred owner side. Hence, we agree with Mendola and Fesi that the occlusion cues and the stereo cues are integrated in BOWN computation. The "serrated edge illusion" figures (Anderson) are completed differently depending on the polarity of stereo-disparity given to the image. It is possible that the BOWN computation creates different depth orders and completions by finding the most coherent answers of ownership reflecting both occlusion and stereo cues. Therefore, in principle, the observation is not against our approach but rather confirms that globally coherent BOWN computation is the key to determine completion.

REPRESENTATION OF MODAL AND AMODAL COMPLETION

In amodal completion, we do not see the occluded part but still have a vivid perception that the occluded surface continues behind the occluder. How does the visual system establish such a perception? The common explanation of this phenomenon is an interpolation of intersecting contours by connectability (Fantoni and Gerbino). We have a different view. First, a higher level computes the likelihood of the shape of surfaces. Next, amodally completed surfaces are only represented at the higher level. Only in modal surfaces, the feedback signals travel down to the lower level and the contour signals are activated. In this way, modal contours are realized. The responses of neurons at illusory contours (von der Heydt et al., 1984, IC neurons hereafter) correspond to this activation.

In Figure 2, a rectangle with sine wave contours is partially occluded. In A and B, the position of the occluder is slightly shifted vertically. This creates different "connectability" relationships of intersecting segments (see Figure 2C and 2D, red dashed lines). Therefore, predicted interpolations would differ in these two figures, which does not correspond to the perception. Furthermore, if two identical rectangles overlap orthogonally (see Figure 2E, left), interpolation creates borderlines (right) converting T-junctions to X-junctions. The visual system, then, has to compute the depth order from the five segmented areas. This does not appear to be the most parsimonious computation compared to an approach detecting T-junctions first and computing depth order accordingly. In our view, the shapes of these occluded surfaces are represented at the higher level, a sine wave rectangle and a rectangle, respectively, without articulate point-by-point line drawings of their contours.

NEURONAL CLASSES INVOLVED IN BOWN COMPUTATION

Abutting gratings and the Ehrenstein figure that von der Heydt pointed out, as well as other figures with line

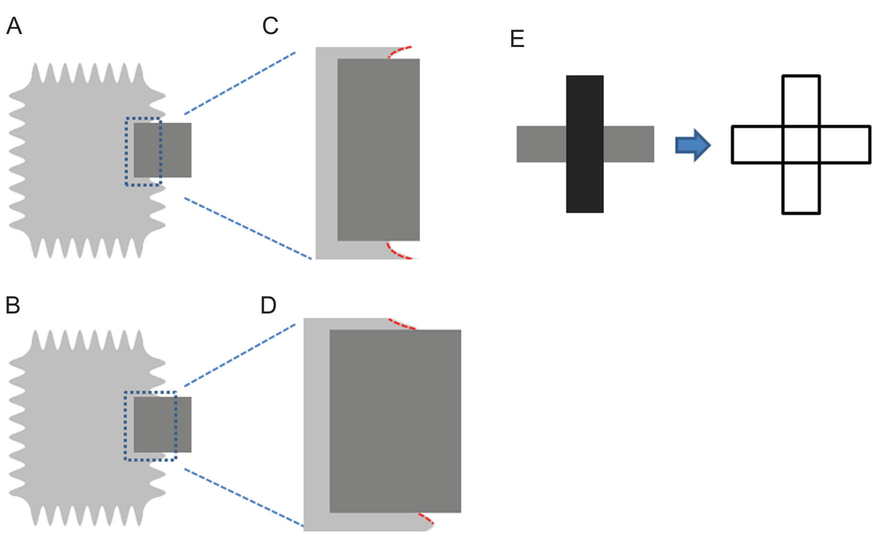

Figure 2. In A and B, a rectangle with a sine wave contour is partially occluded by a small rectangle. In B, the position of the occluder is slightly shifted down. The perception of amodal completion in the two images is not affected by this difference. However, as shown in the magnified image in C and D, the connectability of the line segments (red dashed lines) is quite different. E: Two overlapping identical rectangles creating amodal completion (left). With an interpolation algorithm, the borderline map would be as shown on the right, creating five segmented rectangles. While the T-junctions in the original image, crucial information of depth order, are lost, the interpolation approach necessitates depth order computation based on this borderline map.

endings (Fantoni and Gerbino), all suggest that end-stopped (ES) signals may have a special meaning for perceptual organization. Importantly, an ES signal often implies an occlusion by a contour orthogonal to the line (von der Heydt). This suggests that ES signals are specifically grouped on the bases of the implied depth order. Therefore, although we have not implemented ES signal detection in our DISC model, it is possible to incorporate it as an additional cue to the BOWN computation.

Von der Heydt pointed out that the neurophysiological data suggest that IC neurons and BO neurons are not identical. He showed that neurons responding to abutting gratings and those responding to Kanizsa illusory contours are identical. Because the abutting gratings do not create clear BOWN, this finding may suggest that IC neurons are not BO neurons. However, when the depth order of two abutting surfaces is ambiguous, it is possible that BO neurons still create action potentials (the activity levels of two neurons competing for the owner side would be identical in such cases). They would create illusory boundary perception with ambiguous ownership. The data showing that the range of distal interaction differs in BO neurons and IC neurons also suggest that they belong to two separate classes. However, the data also suggest another possibility. The difference may be due to the fact that stronger synaptic inputs are necessary to create action potentials in IC neurons. Note that, when BOWN signals were measured, the physical boundary was given to the receptive field of the neuron. On the other hand, when a neuron responds at the location of illusory contour, there is no boundary signal coming from the lower level. Hence, the membrane potential of the neuron may be less depolarized due to the lack of the direct input, even if it receives synaptic inputs by the global interaction circuit for BOWN computation.

The visual system is robust, showing a wide range of context sensitivities as the commentators pointed out. We believe that the neural mechanism of BOWN computation and its link to the illusory surface perception, as our paper argued, is the key starting point to investigate the emergent global property of figure-ground organization within a dynamic hierarchical feedback system.

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