BRILL

Seeing and Perceiving 23 (2010) 295–333

SEEING AND PERCEIVING
brill.nl/sp

Probing Perceptual Antinomies with the Watercolor Illusion and Explaining How the Brain Resolves Them

Maria Tanca[1], **Stephen Grossberg**[2] **and Baingio Pinna**[1,*]

[1] Department of Architecture, Design and Planning, University of Sassari, Palazzo del Pou Salit,
Piazza Duomo 6, 07041 Alghero (SS), Italy
[2] Department of Cognitive and Neural Systems, Center for Adaptive Systems, and Center of
Excellence for Learning in Education, Science and Technology, Boston University, Boston,
Massachusetts 02215, USA

Received 12 October 2009; accepted 23 July 2010

Abstract

The purpose of this work is to study how the brain solves perceptual antinomies, induced by the watercolor illusion in the color and in the figure–ground segregation domain, when they are present in different parts of the same object. The watercolor illusion shows two main effects: a long-range coloration and an object–hole effect across large enclosed areas (Pinna, 1987, 2005, 2008a, b; Pinna and Grossberg, 2005; Pinna *et al.*, 2001). This illusion strongly enhances the unilateral belongingness of the boundaries (Rubin, 1915) determining grouping and figure–ground segregation more strongly than the well-known Gestalt principles. Due to the watercolor illusion, both the figure and the background assume new properties becoming, respectively, a bulging object and a hole both with a 3-D volumetric appearance (object–hole effect). When the coloration and the object–hole effects induced by the watercolor illusion are opposite (antinomic) within different portions of the same shape, some questions emerge: Do the antinomies split the shape in two parts (a half shape appears as an object and the other half as a hole) or are they solved through a new emergent perceptual result beyond the single effects? Is there a predominance of one component over the other that is less visible or totally invisible? What is perceptible and what is invisible? Is there a wholeness process under conditions where perceptual antinomies coexist? By imparting motion to a watercolored object that gradually should become a hole while overlapping another object placed behind, is the wholeness of the watercolor object weakened or reorganized in a new way? The results of phenomenological experiments suggested that the antinomies tend to be solved through two complement processes of phenomenal wholeness and partialness. These processes are explained in the light of the FACADE neural model of 3-D vision and figure–ground separation (Grossberg, 1994, 2003), notably of how complementary cortical boundary and surface representations interact with spatial attention to generate conscious percepts of 3-D form and motion.

---

[*] To whom correspondence should be addressed. E-mail: baingio@uniss.it

DOI:10.1163/187847510X532685

Keywords
Neural model, grouping principles, Gestalt psychology, watercolor illusion, transparency, figure–ground separation, stratification, bipole cells, competition, complementary consistency, FACADE theory

1. Introduction: The Watercolor Illusion

The watercolor illusion consists of coloration and object–hole effects (see Fig. 1). The former is a long-range assimilative spread of color emanating from a thin colored edge — orange — lining a darker chromatic — purple — contour. The latter is a strong enhancement of the unilateral belongingness of the boundaries (Rubin, 1915) where both the figure and the background appear respectively as a bulging object and as a hole with a 3-D volumetric appearance (Pinna, 1987, 2005, 2008a; Pinna and Grossberg, 2005; Pinna *et al.*, 2001).

In Fig. 1(a), the orangish coloration effect spreads uniformly over the frame that appears bulging like a bas-relief. Contrariwise, the inner tilted square appears like a 3D hole with a cold white color or very slightly purplish. By reversing purple and orange contours (Fig. 1(b)), both the coloration and the object–hole effects reverse accordingly. The inner hole becomes an orangish volumetric tilted square shape, seen like an island or an object floating in the empty space, and the frame of Fig. 1(a) is now perceived like an empty three-dimensional space surrounded by a filled surface solid like the tilted inner square shape.

It is worthwhile noticing that the object–hole effect of Fig. 1(a) clearly demonstrates that the watercolor illusion is pitted and prevails against the Gestalt factors

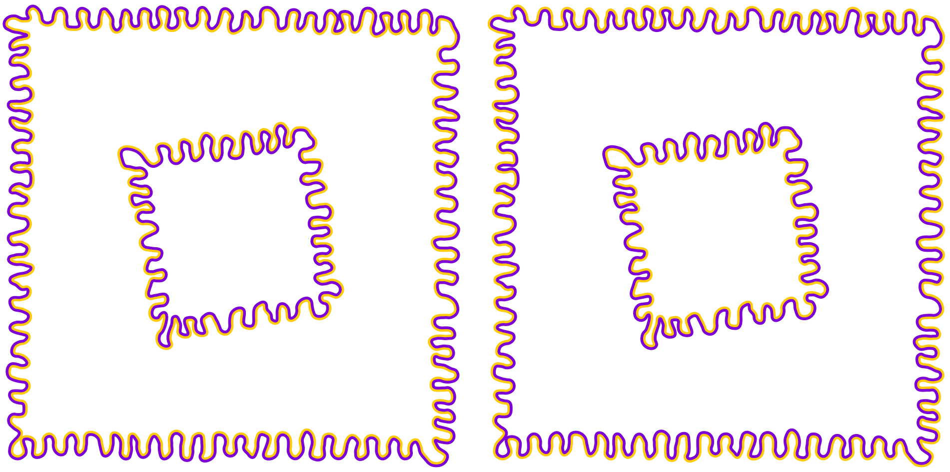

(a) (b)

Figure 1. *The watercolor illusion*: (a) the orangish illusory coloration spreads uniformly over the frame that appears bulging like a bas-relief. By reversing purple and orange contours (b), both the coloration and the object–hole effects reverse accordingly. This figure is published in colour on http://brill.publisher.ingentaconnect.com/content/vsp/spv

of surroundedness (Rubin, 1915, 1921) and relative orientation (Bozzi, 1975). It has been shown (Pinna *et al.*, 2003) that the watercolor illusion and its luminance profile along the boundary contours can be considered as a principle of figure–ground segregation distinct and more effective than all the known gestalt principles (see Pinna, 2005, 2008a).

Given its strong effects, the watercolor illusion is a good tool to investigate how the visual system extracts basic information about the wholeness of an object, and more specifically about its coloration and object–hole effects, starting from its boundaries. It was suggested that the necessary information, needed to define the figural attributes like shape, color and depth, are placed on the boundaries and, more particularly, in the luminance gradient profile (Pinna, 2008a; Pinna and Reeves, 2006). From the boundaries these properties fill the whole shape (Grossberg and Mingolla, 1985; Grossberg and Swaminathan, 2004; Grossberg and Todorovic, 1988; Grossberg and Yazdanbakhsh, 2005; Grossberg *et al.*, 2007).

The main purpose of this work is to use the watercolor illusion to understand the problems of filling-in and visual wholeness when antinomic kinds of attributes are induced along the same boundary contours. The main questions are: Do the antinomies split the shape in independent parts (a half shape as an object and the other half as a hole) or are they solved through a new emergent perceptual result beyond the single effects? Is there a predominance of one component over the other, which is less visible or totally invisible? What is perceptible and what is invisible? Is there a process of wholeness that solves the antinomies or under whose conditions perceptual antinomies coexist? By imparting motion to a watercolored object that switches to a hole, is the wholeness of the watercolor object weakened or reorganized in a new way? Can motion imparted to the watercolor illusion contribute to understand the problem of phenomenal wholeness and its main attributes: homogeneity, continuity, univocality, and belongingness?

There are many other experimental approaches to understanding how the brain may resolve such perceptual antinomies, ranging from psychophysical visual displays, such as those of perceptual stratification (Kanizsa, 1985; Kelly and Grossberg, 2000), to artistic works such as those of M. C. Escher. The watercolor illusion in its manifold variations provides a powerful new probe of such paradoxes due to its ability to induce the brain to complete large ambiguous regions of an image using context-sensitive interactions between boundary and surface formation processes which lead to strong percepts of illusory color filling-in. In this regard, the watercolor illusion is similar to neon color spreading. Indeed, key properties of both the watercolor illusion and neon color spreading have been explained in a unified way using the FACADE model of how the visual cortex generates 3D boundary and surface representations (Pinna and Grossberg, 2005). FACADE neural mechanisms will also be used below to explain the new effects that are reported in this article.

2. General Methods

In order to define appropriately the phenomenal properties of the antinomic stimuli suggested, we used two suitable methods. Firstly, a phenomenological free-report method, the same used by Gestalt psychologists, in which ‘naïve’ subjects are given a series of visual stimuli and asked to report anything they see. Secondly, the free-report method is supplemented by a more quantitative one, where subjects are instructed to rate (in percent) the magnitude estimation of the descriptions obtained in the phenomenological experiments.

2.1. Subjects

For each stimulus, independent groups of 15 undergraduate students participated to the phenomenological experiments. Subjects were naive as to the purpose of the experiments, and all had normal or corrected-to-normal acuity.

2.2. Stimuli

The stimuli, composed of the figures illustrated and described in the next sections, were presented on a computer screen with ambient illumination from a Osram Daylight fluorescent light (250 lux, 5600°K). The stroke width was approx 6 arcmin. The luminance of the white background was 88.3 cd/m^2. Black contours had a luminance contrast of 0.97 (luminance value of 2.6 cd/m^2). The CIE chromaticity coordinates for the main colors used were: (purple) 0.30, 0.23 and (orange) 0.57, 0.42.

The stimuli are created using Adobe Illustrator with color settings for RGB space (sRGBIEC61966-2.1). All stimuli were displayed on a 33 cm color CRT monitor (Sony GDM-F520 1600 × 1200 pixels, refresh rate 100 Hz), driven by a MacBook Pro computer with an NVIDIA GeForce 8600M GT. The monitor was calibrated using a Minolta colorimeter (CS 100 Chroma Meter) and procedures set out in Brainard *et al.* (2002).

All stimuli were displayed in a frontoparallel plane at a distance of 50 cm from the observer and were viewed binocularly. A chin rest stabilized the head position of the observer.

2.3. Procedure

2.3.1. Phenomenological Experiments

The subjects’ task was to report spontaneously what they perceived by giving, as much as possible, an exhaustive description of the main visual properties. Unless otherwise stated, different groups of 15 naive observers each described only one stimulus. This was done to avoid interactions and contaminations among stimuli. The descriptions reported in angle quotes (guillemets — «») through the paper used similar phrases and words as those provided by the spontaneous descriptions of no less than 12 out of 15 subjects in each group but edited for brevity and representativeness. Three graduate students of linguistics, who were naive as to the hypotheses, judged the edited descriptions and provide a fair representation of those provided by the observers. The descriptions, incorporated within the text, aid the reader during the stream of argumentations. In the two kinds of experiments, each stimulus was presented once to each observer. Observation time was unlimited. All the reports were quite spontaneous.

2.3.2. Scaling Experiments

New groups of subjects were instructed to rate the accurate reflection (in percent) of the descriptions of the phenomenological experiments, i.e., the degree to which it captures the phenomenon being rated. An example of the task is: ‘please rate whether this statement is an accurate reflection of your perception of the picture, on a scale from 100 (perfect agreement) to 0 (complete disagreement)’. Throughout the text, each description is followed by the result of the magnitude estimation (mean rating) compared to other possible phenomenal results.

In the two kinds of experiments, each stimulus was presented once to each observer. Observation time was unlimited. All the reports were spontaneous.

3. Visual Antinomies Due to the Watercolor Illusion

3.1. From Antinomies to the Three Dimensional Wholeness

In Fig. 2(a), a combination of Fig. 1(a) and 1(b) with chromatic contours reversed in the two halves is illustrated. The two halves are perceived with opposite coloration and object–hole effects. The filling-in of «the two effects of the watercolor illusion is confined within the boundaries of one half and does not reach exactly the

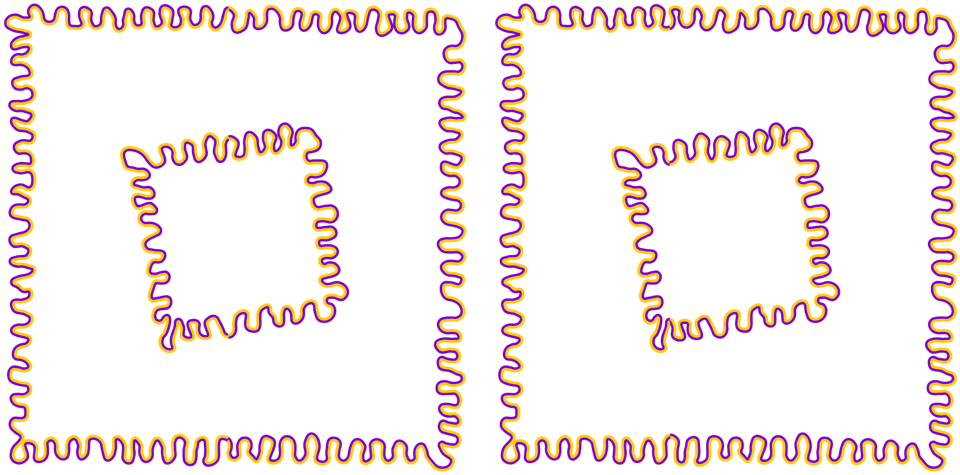

(a) (b)

Figure 2. A combination of Fig. 1(a) and 1(b) with chromatic contours reversed in the two halves shows opposite coloration and object–hole effects, and a global three-dimensional folding with the right half of the inner square and the left half of the frame emerging from the background. By increasing the size of one half against the other the results do not change. This figure is published in colour on http://brill.publisher.ingentaconnect.com/content/vsp/spv

middle point of each half but it stops earlier» (mean rating 100%). This result is likely due to the antinomic opposition of the effects, which reinforces and increases the separation between the left and right halves. Phenomenally, «one half of the inner wiggly square appears as a background and the other half as a figure and *vice versa* to the frame» (98). This suggests that each filling-in effect is driven by local factors of color and object–hole organization depending on the luminance profile along the boundary contours. This contraposition of effects creates «a global three-dimensional folding with the right half of the inner square and the left half of the frame emerging from the background» (89). When the subjects were asked to describe how exactly the folding occurred, they could not describe it precisely. In fact, no folding can explain the object–hole reversion. However, they continued to perceive the global folding even if they could locally perceive the antinomic coloration and object–hole effects.

These results demonstrate that the antinomic effects in the two regions of the figure are processed as a three-dimensional whole. Whole and part perceptions coexist although they cannot be logically integrated. Only within the whole perception are the antinomies solved. More generally, the process of wholeness puts together the two halves in a new and more complex way. The question is then: how are antinomies put together and which are the emerging new perceptual properties that phenomenally solve the local antinomies present in the stimulus? This question is not trivial; in fact theoretically, the antinomies might have remained separated and in reciprocal contradiction or one might have prevailed over the other, then annulling the perception of the weaker one. These are only two among many other possible theoretical results expected under these conditions.

By increasing the dimension of one half against the other, as illustrated in Fig. 2(b), in spite of its predominance, «the same 3D solution of Fig. 2(a) is perceived again» (91). This result is expected on the basis of the idea that the necessary information, needed to define the figural attributes like shape, color and depth, is placed on the boundaries. As a consequence, the information of these attributes spreads from the boundaries and stops where and when a different or opposite kind of information is reached.

It is worth noticing that by comparing both the coloration and the object–hole effects of Figs 1 and 2, in Fig. 2 the antinomic effects within the same form «reduce their strength, i.e., the filling-in of both coloration and object–hole effect is not only reduced in space but also in strength becoming weaker and weaker» (82). This global reduction occurs «both in the figure and in the background region, therefore also the perception of the hole is weaker in Fig. 2 than in Fig. 1» (83).

3.2. Paradoxical Transparency

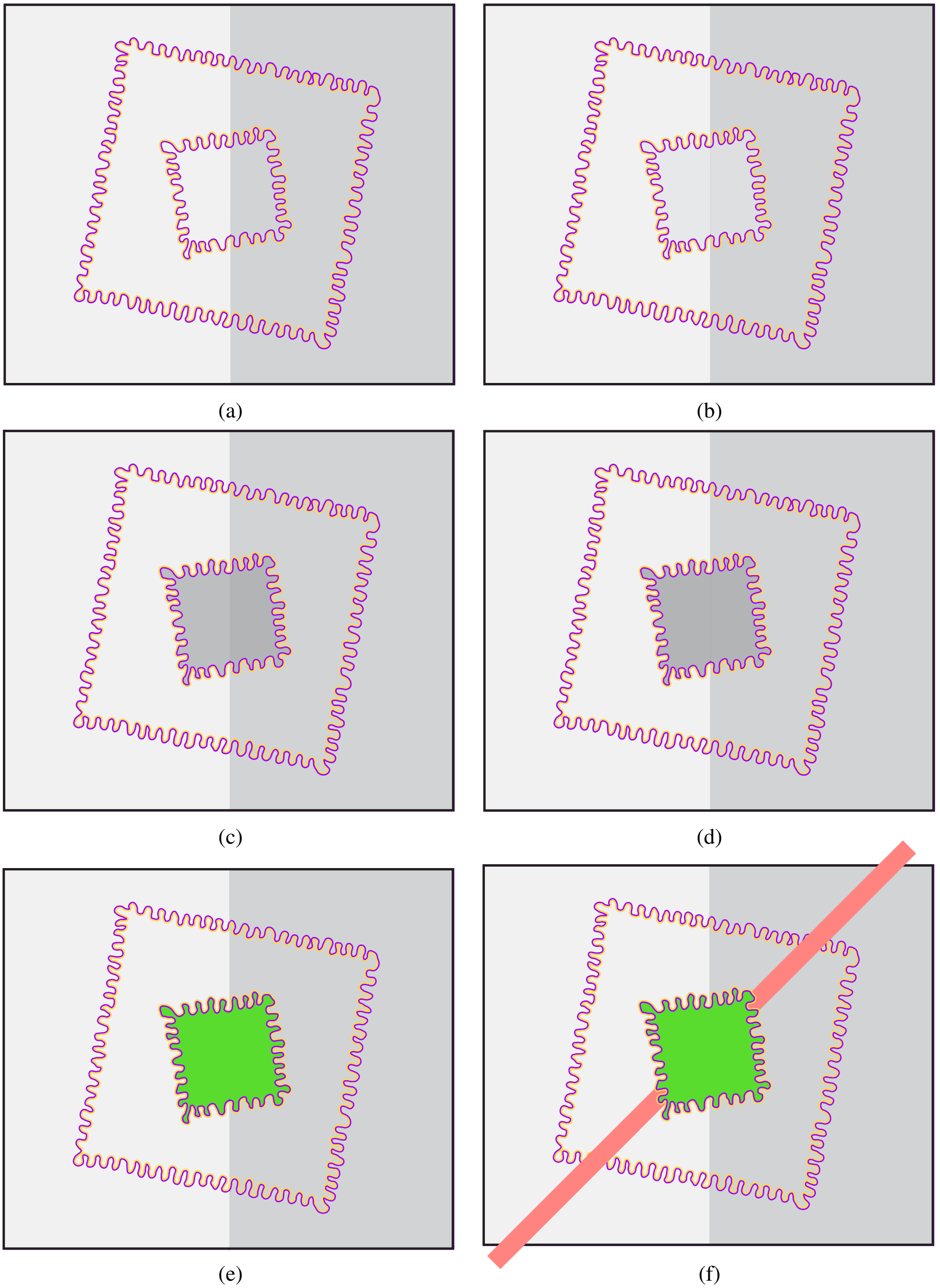
A second way to study visual wholeness through antinomies placed on the same figure can be obtained by inducing object status (figural clues) to the hole created by the watercolor illusion. Although the watercolor illusion is characterized by an opaque figural effect, whose inner coloration has epiphanous and surface color properties, the resulting watercolored surface can become «transparent» (100) under conditions like those illustrated in Fig. 3(a).

«The frame appears as a figure and the inner tilted square as a hole» (98). The coloration within the light and dark gray rectangles induces a transparent effect of the frame. «While the inner small square appears as an empty space (a hole) completely transparent, the frame appears as having a certain amount of density (transparency <100%)» (97). The question is now: can the density of the transparent hole, be pitted against the effect produced by the watercolor illusion? In other words, if the empty hole induced by the watercolor illusion is counterbalanced by figural clues, how does the visual system put together this antinomic information?

Figure 3(b) and 3(c) shows clearly that by making the inner surface of the small square of Fig. 3(a) denser and denser, i.e., less and less transparent than the frame, «the square continues to appear as a hole, although it is seen denser» (92). «The contradiction is not perceived at all» (0). It is not perceived also when «it reaches the extreme limit of complete opacity (100% dense, Fig. 3(d))» (0). Despite its opacity and in spite of the amodal completion of the line dividing the two rectangles with different luminance contrast, «the inner square still appears as a hole in relation to the watercolored frame» (90). Controls (not illustrated), made with only purple contours, «annul the hole effect induced by the watercolor illusion» (100).

In Fig. 3(e), «the antinomy is weakly perceived even when the inner square is green: it appears opaque but at the same time as a hole» (28). The chromatic differentiation, which is a strong figure–ground principle, under these conditions does not win against the watercolor illusion. However, «different ways of perceiving (local and global) in different spatial location of the inner square elicit switches or reversions of the perception from hole to object» (95). It is worthwhile noticing that under these conditions, the amodal completion factor works powerfully, due to the interrupted line of the boundary between the two different halves of the gray background. This line appears to complete amodally behind the small green square. This condition should enhance the figural property of the inner square and not the one of the frame, where the amodal completion of the line does not work. This implies a summation between the chromatic differentiation and the amodal completion.

The figural effect of the frame due to the watercolor illusion makes the depth segregation of the inner square paradoxical. More precisely, as for the perceptual division of the two rectangles due to variations in luminance contrast, «the inner square is perceived at the same time as a hole, when referred to the watercolored frame (the figural effect imposed by the watercolor illusion is strong enough to counteract the local perception of the inner square as a figure), and as an opaque surface when referred to the gray division and to its differentiated chromatic opacity» (89). However, when the perceptual results concern different references (frame and luminance division), the paradox is solved and not perceived at all because the antinomy is accounted for by opposite but local figure–ground and depth segregation. In other words, «the two opposite effects are local cues and depend on the way the figure is observed» (92).



(a) (b) (c) (d) (e) (f)

Figure 3. (a) A transparent watercolor illusion with the inner square as a hole. (b)–(d) The square continues to appear as a hole, although it is seen denser and denser and it reaches the complete opacity or (e) when it is green. (f) The oblique red bar is perceived to amodally complete behind the inner green square. However, by moving the gaze around the junctions, the figural effect induced by the watercolor illusion is restored. This figure is published in colour on http://brill.publisher.ingentaconnect.com/content/vsp/spv

In Fig. 3(f), «the oblique red bar is perceived to amodally complete behind the inner green square» (100). «This result is much stronger at global viewing and can be better perceived when the gaze follows the oblique direction of the bar» (100). However, when the gaze moves around the boundary contours of the inner square «the stronger object–hole effect of the watercolor illusion emerges» (92). Under these conditions, the antinomy is «more clearly perceived» (40).

Although the amodal completion can reverse the figure–ground organization of the small square, «it is effective only at a short distance; i.e., near the T-junctions» (88). «By moving the gaze a little further around the junctions, the figural effect induced by the watercolor illusion is restored» (90). The local results emerging from these figures are not really perceived in contradiction, but they are different results coming from different points of view, that do not necessarily have to be logically integrated into a unique and homogeneous global percept.

Figure 3(a)–(f) suggests that, differently from Fig. 2 where a process of wholeness puts together the two halves in a three-dimensional whole, the phenomenal wholeness puts together the antinomies that are not perceived in direct contradiction but as results of different ways of seeing. In other words, these results demonstrate that even if different kinds of clues are perceived, either due to the amodal completion or to the watercolor illusion, the contradiction between them is not necessarily seen. This suggests that the process of figural wholeness does not tend to include or acknowledge inner or direct contradictions, which are instead placed at different levels of perception or considered as belonging to different ways of seeing.

3.3. Paradoxical Chromatic and Object–Hole Organization

A third way to create antinomic properties through the watercolor illusion is to play with the reversal coloration and object–hole effects obtained by reversing the luminance contrast of the background, e.g., from white to black, while the luminance contrast of the contours is kept constant (Pinna and Reeves, 2006). In Fig. 4, «purplish stars at the top and orangish crosses at the bottom are perceived» (100). Moving the gaze from the bottom to the top of the figure, «the orangish crosses become purplish stars» (100). The antinomic results are perceived as shape transformation in space, but at a global and first view neither the transformation nor the antinomic object–hole organization are noticed. This result is in contrast with Rubin's claim that the currently figural region is maintained even on black/white reversal (Rubin, 1921).

In Fig. 5, at a first sight, «the two figures appear alike showing a transparent object» (92), but in the two halves the purple and orange contours are respectively in continuation (purple with purple and orange with orange in Fig. 5(a)) or in cross-continuation (purple with orange and orange with purple in Fig. 5(b)). These two conditions are not clearly perceived opposed, but «a chromatic-figural homogeneous organization is perceived within each frame» (89). «The precise specific perceptual result depends on the part of the figure that is observed as first. Therefore, «it can change» (82). After a deeper and more local observation, when the

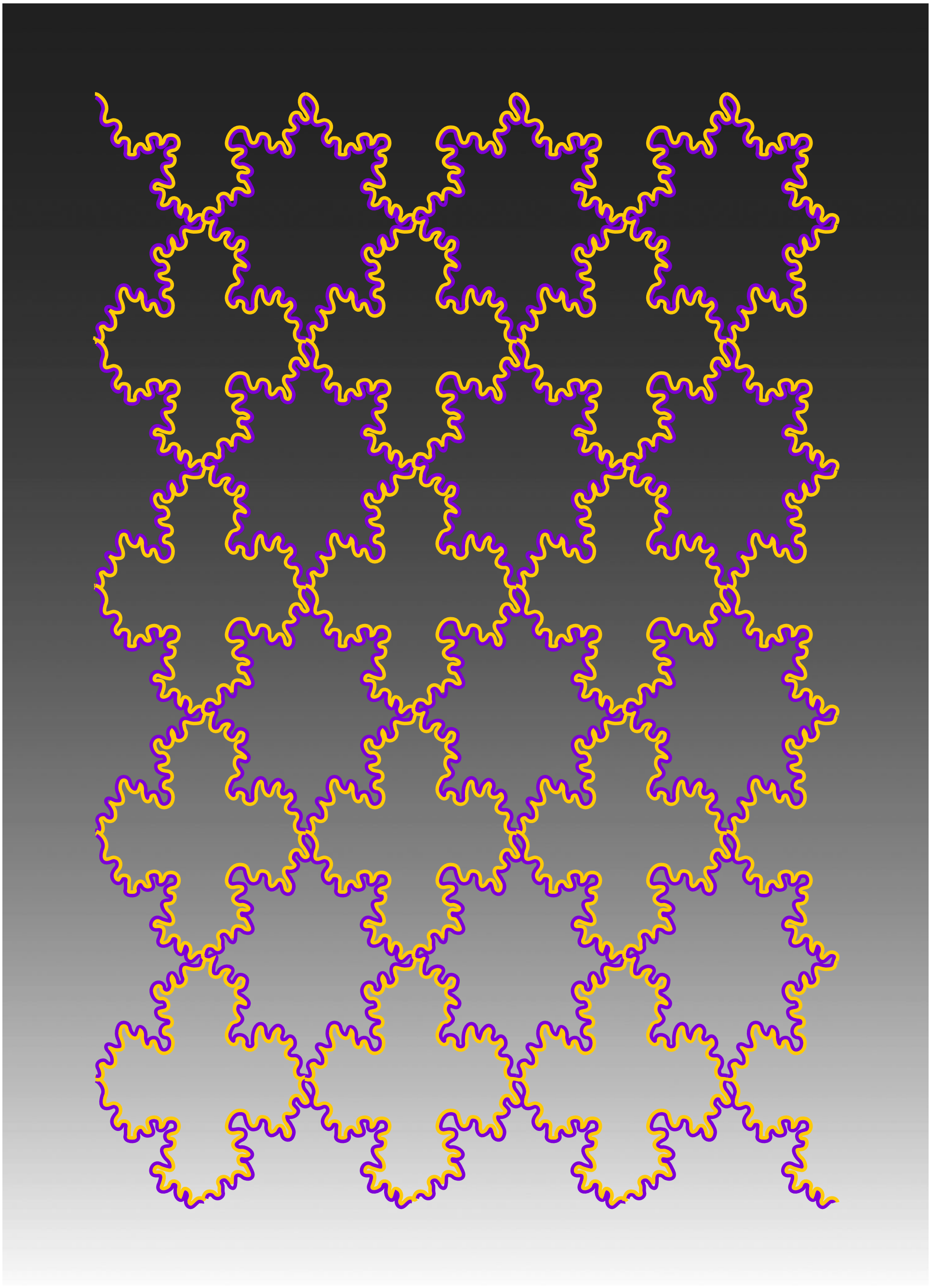
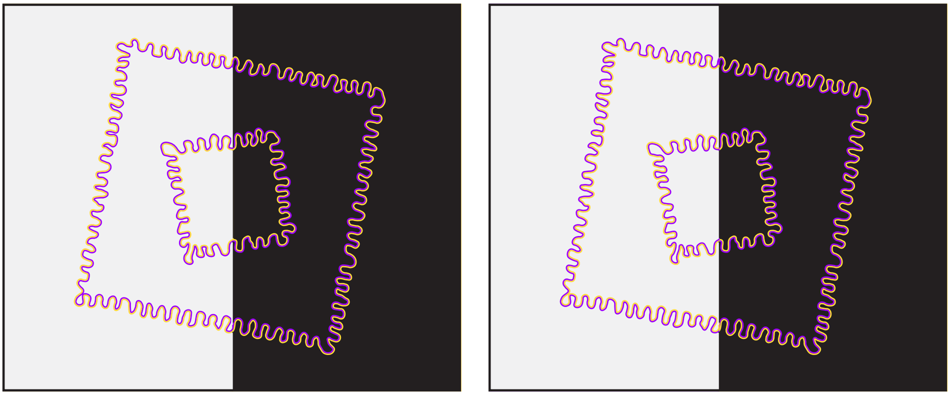


Figure 4. Orangish crosses at the bottom become purplish stars at the top. This figure is published in colour on http://brill.publisher.ingentaconnect.com/content/vsp/spv

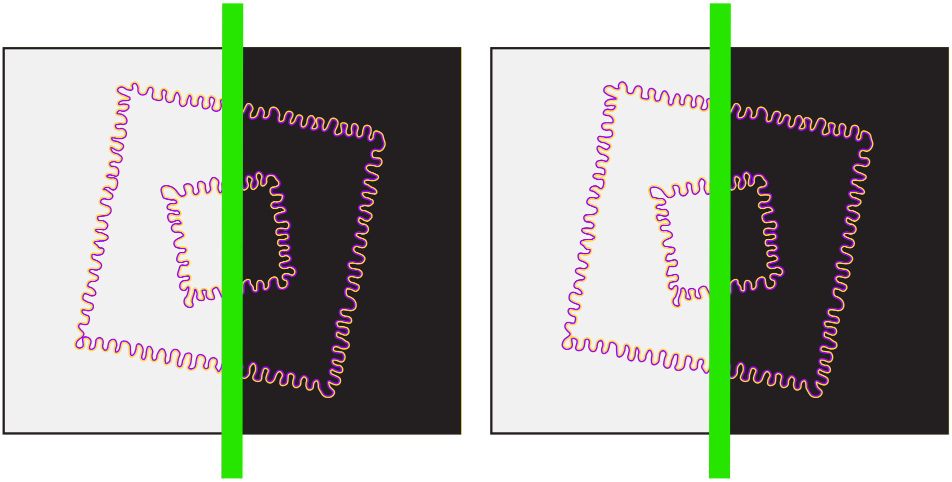


(a) (b)

Figure 5. In (a) opposite object–hole effects and the same chromatic colorations are perceived in the two halves, while in (b) the same object–hole effects and different colorations are seen in the two halves. At a holistic view none of these antinomies is perceived. This figure is published in colour on http://brill.publisher.ingentaconnect.com/content/vsp/spv

purple and orange contours are in continuation, because of the reversed contrast of the two halves, «while within one half (right) the frame appears as a bulging purplish figure, within the second half (left), the frame appears as a background or as an empty space» (73). When they are in cross-continuation, due to the reversed contrast of the two halves, «if within one half (left), the frame appears slightly orange, within the second half, it appears bluish (right)» (70). Under these conditions the figure–ground organization is not reversed as in Fig. 5(a). In summary, in Fig. 5(a) opposite object–hole effects and the same chromatic colorations are perceived in the two halves, while in Fig. 5(b) the same object–hole effects and different colorations are seen in the two halves. «At a holistic view none of these antinomies is perceived» (0) as though the wholeness of the frame were driven by some kind of chromatic and object–hole homogeneity assumption that shows as an emergent result «the transparency of the frame or of the inner square» (98). When the emergent holistic transparency and the local antinomies are perceived, «they are not perceived in contradiction but as results of two ways of seeing. One result does not influence the other» (90).

The opposite phenomenal results between coloration and object–hole effects in the two halves can be «more clearly and univocally noticed» (65) when a colored stripe is superimposed to the line separating the two halves as illustrated, respectively, in Fig. 6(a) and 6(b). Under these conditions, the colored stripe creates a clear amodal separation between the two halves that favors the perception of the differences and inhibits the *wholeness filling-in* of the two effects of the watercolor illusion and then the tendency to the homogeneity of the figural attributes within a whole figure. Given that the phenomenal belongingness of the two halves to the same figure and then the wholeness of the components are weakened by the stripe, the differences and the antinomies are strengthened similarly to Koffka–



(a) (b)

Figure 6. The opposite phenomenal results between coloration and object–hole effects in the two halves of Fig. 5 can be more clearly and univocally noticed when a colored stripe is superimposed to the line separating the two halves. This figure is published in colour on http://brill.publisher.ingentaconnect.com/content/vsp/spv

Benussi ring (Koffka, 1915). Under these conditions, a gray homogeneous ring, placed in-between a black and white background, and divided by a line or a stripe, does not appear homogeneous. The inducing contrast effects of the backgrounds are strengthened. These results demonstrate that the belongingness is strongly related to the phenomenal wholeness.

Phenomenally, Fig. 5 differs from Fig. 2, even if the main kind of antinomy is very similar, i.e., two halves with opposite coloration and object–hole effects. The reverse contrast between contours and background in the two halves introduces a further kind of antinomy, which makes the global three-dimensional folding of Fig. 2 more difficult or impossible, although it elicits the phenomenal transparency. Under these more complex circumstances the problem of whole perception, starting from antinomic local information, emerges more clearly. If in Fig. 2 the filling-in of watercolor attributes appears «confined to only one half of the stimulus» (100), in Fig. 5 it seems «to ‘fill’ the entire frame» (91) as it is also suggested and further corroborated by the results of Fig. 6.

Figures 5(a) and 6(a) suggest that antinomic properties within the same figure can be invisible at a first sight by showing phenomenal transparency and can be visible only after a more analytical observation where the whole transparency is destroyed. The homogeneity of coloration and object–hole attributes appears to be as a basic assumption or as an essential requirement of the visual process of wholeness. This homogeneity assumption is related to the filling-in process and to the phenomenal belongingness as demonstrated by Fig. 6.

It is worthwhile remarking that the local perception of the antinomies does not destroy the holistic perception of uniform and homogenous transparency. They appear to be independent; in fact subjects «can switch from one to the other way of seeing without influencing significantly their perceptions» (82).

3.4. Antinomies and Wholeness During Motion

The antinomic conditions illustrated in Fig. 5 show static sets of dichotomic properties that cannot tell us anything about how the phenomenal wholeness is perceived in time. A more complete understanding of this problem can be obtained by imparting motion to the watercolor shape that should pass through at least three main transitional phases: (i) one where the watercolor shape is univocally perceived as a colored object, (ii) one where half of it is perceived as an object and half as a hole, and (iii) one where the watercolor shape is univocally perceived as an empty hole. Under these conditions, the motion of the watercolor shape, even if moving through different phases, should play a significant role in unifying the three phases. Motion is supposed to induce homogeneity, continuity, univocality, belongingness and wholeness. In fact, if motion induces these properties, they should also be induced in the antinomic phases (the first and the third previously mentioned), but if this is true, this implies a logical paradox. The questions are: which is the solution of this antinomy and how does the wholeness change while the moving component crosses the three phases and particularly the antinomic ones? In other words, given that there are at least two antinomic univocal wholeness (the two extreme phases), if motion imparts continuity to the wholeness, how are they put together during the motion of the watercolored shape and which is the final whole result?

To answer these questions static and dynamic stimuli were compared. In Fig. 7, the three possible phases are illustrated statically. In the first row, the wiggly watercolor shape is clearly perceived as «an object (left) or as a hole (right)» (100). In the middle row, the watercolor shape intersects in about its center the black rectangle that reverses the luminance contrast of the chromatic contours and then the coloration and object–hole effects. Phenomenally, «at first sight the holistic observation of the figure placed on the left of the row reveals homogeneous watercolor effects on a transparent shape», but «a deeper and local observation shows that half of the wiggly shape appears as an orangish object (left) and the other half as an empty hole (right)» (84) and «*vice versa* as for the figure on the right of the row» (85). In the third row, the wiggly watercolor shape is perceived univocally as «a hole (left) or as an object (right)» (100), i.e., contrariwise to the first row.

By imparting motion to the static watercolor shape, the specific questions derived from the previous ones are the following: are the antinomies still perceived? How are these static different solutions and antinomies put together? Is there any interruption in the continuity, homogeneity and univocality of the whole shape? The answer to these questions is related to a recent work (Pinna and Tanca, 2008), where a figure–ground principle, called 'motion *vs* stationary', was enunciated. This principle states: 'all else being equal, moving elements appear as a figure, while the static elements appear as a background'. In other words, given a static condition with a specific figure–ground organization, the motion imparted to the figure or to

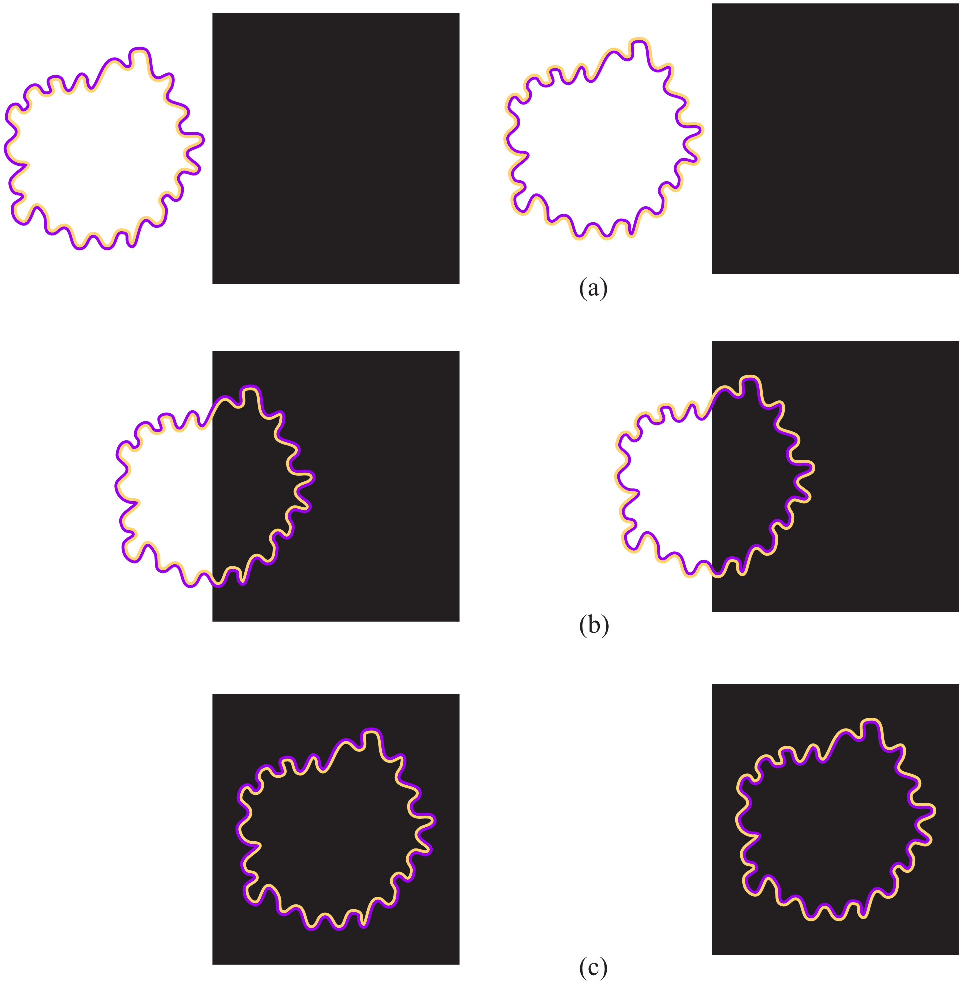


Figure 7. Static and dynamic stimuli, compared under static and dynamic conditions, showing the three possible phases studied. This figure is published in colour on http://brill.publisher.ingentaconnect.com/content/vsp/spv

the background induces a figure status to them, independently from the way they appear under static organization. This principle can be conceived as related to the common fate principle (Wertheimer, 1922, 1923). However, while the common fate is a grouping principle, the moving *vs* stationary is a figure–ground one.

In everyday life it can happen that something, which appears as part of the background under static condition, emerges as a figure when it starts to move. The motion *vs* stationary principle is related to the primary kind of camouflage occurring when a prey animal stands stock-still to avoid predators. Predators use the same kind of camouflage to sneak up on a prey. If camouflage is a form of deception, the moving *vs* stationary principle is exactly the opposite. Therefore, if the stationary condition elicits the camouflage, then the motion instills figurality.

It was demonstrated (Pinna and Tanca, 2008) that, when motion is imparted to watercolor holes, they are perceived as moving holes and assume a strong figure status. In other words, rather than being switched as moving objects, they appear much more strongly as holes. This result implies that motion supports and favors synergistically the hole status induced by the watercolor illusion, although it should apparently and logically behave contrariwise. In other words, the motion *vs* stationary principle operates by summing the figurality it instills to the object–hole segregation induced by the watercolor illusion. Along the same lines, we suggest that motion strengthens figurality and wholeness attributes (homogeneity, continuity, univocality and belongingness) induced by the watercolor illusion. More precisely, besides inducing a further figure status to a watercolored hole, motion strengthens the wholeness of the watercolor shape even when antinomic results are expected from a logic point of view. As a consequence, it favors the wholeness dynamic of putting together antinomies under watercolor conditions.

These predictions suggest the phenomenal distinction between the unity/oneness of an object and its multiplicity/heterogeneity. While the oneness is supposed not to be antinomic, the multiplicity of its component parts might be. As a consequence, on the basis of the moving hole results (Pinna and Tanca, 2008), we suggest that motion should strengthen the phenomenal wholeness and then the oneness of the watercolored object even if multiple antinomic specific instances of it in different spatial or temporal locations can also occur at the same time. These two phenomenal levels should not annul each other nor appear in contradiction.

The stimuli used were those illustrated in Fig. 7: the watercolored shapes were translated and/or rolled with a speed of ∼1.5°/s. The starting points of each kind of motion were the two extreme positions illustrated in Fig. 7, i.e., outside and inside (from the center of) the rectangle. The space covered during motion stops after having run the three positions: outside, intersection and inside. Two new groups of subjects were used for the dynamic condition. The subjects' task of the first group was to give an exhaustive description of the main visual properties of the moving watercolored shape, and to scale the relative strength or salience (in percent) of the perceived results. After this *first test*, a new group of subjects were experienced with some examples of watercolor illusion by showing them instances of coloration and object–hole effects different from those of the test. Afterwards, they described and judged a new random stimulus combination (*second test*). The purpose of the two tests was to favor the first sight and more global view *vs* the deeper and more analytical one. Each combination of stimuli was presented once and in a different random order for each observer.

3.4.1. First Test

Before experiencing the watercolor illusion, when the watercolor shape was perceived as an object and started moving from the external position (left on the first row of Fig. 7) toward the center of the black rectangle, at a global view it appeared as «a dense watercolor object» (100) and it was perceived as such until it intersects the rectangle, where it was seen as «transparent (∼15% density)» (100). Only when it approached the center of the rectangle it was poorly perceived as «a hole (2 subjects out of 15)» (5). This implies some kind of inertia or resistance to variations of the figural status, i.e., from object to hole. No significant differences were reported in the translation and roll motions. «The unity and oneness of the moving shape was never opened to questions» (100). «The antinomies were not perceived at all» (0).

When the watercolor shape was perceived as «a hole and moved from outside (right on the first row of Fig. 7), it became transparent as a hole (0% density) by intersecting the rectangle» (100). Again only by approaching the center of the rectangle, «the hole appeared weakly as an object (4 out of 15)» (7). Again, no significant differences were reported in the translation and roll motions and again «the unity and oneness of the moving shape was preserved along the entire trajectory of the motion» (100). «The antinomies were invisible» (0).

3.4.2. Second Test

After experiencing some instances of the watercolor illusion and perceiving the distinction between coloration and object–hole effect, subjects perceived more clearly the antinomies of the previous conditions but less strongly than in the static conditions (respectively 5 and 15). «The reversion of the object–hole effect was perceived about after halfway along the intersection path between the watercolor shape and the black rectangle» (91). However, «this reversion, even if noticed did not destroy the oneness of the shape» (92). In fact it was seen clearly and totally reversed (the number of subjects perceiving it increases by increasing the size of the intersection path) just after the intersection. In other words, when the watercolor object was perceived as first, it became transparent soon after its intersection with the rectangle (99). «While crossing the intersection region it appeared getting more and more as a hole (the number of subjects increased). It was totally perceived as a hole only after having passed the intersection area» (89). This result demonstrates that the inertia and resistance to changing the figural status is under these conditions less effective than in the first test (respectively 75 and 91). Nevertheless, by reporting this variation of figural status, the subjects were not surprised and the moving shape maintains its uniqueness, homogeneity and continuity (92). Even when the subjects were alerted about the logical antinomy emerging during the trajectory, they reported that «even if they know about this transformation they still perceive a homogeneous whole without any sudden switch of the shape from one figural status (object) to another (hole) or *vice versa*» (88). Also in the second test, motion supports the wholeness of the object but less strongly than in the first test where the antinomies were unnoticed. No significant differences in the phenomenal results were obtained in the two kinds of motion, translation and roll.

When motion started from the center of the black rectangle, the results of the first and second test were quite similar to the ones described before but with the effects reversed, i.e., what was previously perceived as a moving object is now perceived as a moving hole and *vice versa*. We also tested with a new group of subjects a third condition where the total amplitude of the motion was two cycles instead of one, in this way the watercolor shape could be seen going from one extreme (antinomy) to the other (one cycle) and back. It means that the starting and end points were the same. Briefly, the results of the first and second test were very similar to those obtained with only one cycle but under these conditions the variation of the figural status were more clear: respectively 13 and 12 out of 15 noticed the variation of the figural status of the moving shape. Nevertheless, the global homogeneity and phenomenal univocality and belongingness were reported also by most of the subjects (respectively 11 and 13 out of 15).

4. Discussion of Watercolor Effects and Their Implications

The phenomenal results of the four conditions demonstrated that antinomic effects within the same watercolor shape are solved within the more general problem of phenomenal wholeness. Briefly, in the conditions illustrated in Fig. 2, the antinomies within the same shape are processed as a whole in terms of 3D folding even if this is not a logical solution to the coexistence of the antinomies. The phenomenal wholeness, shown in Fig. 3, can make the component parts and the inner antinomies invisible. They are perceived as results of different or specific ways of seeing. Again, whole and part perception coexist even if they cannot be logically integrated. In Figs 4–6, antinomic attributes within the same shape can be invisible at a global view by appearing as phenomenal transparency. They become visible only after a more analytical observation when the transparency is destroyed. The results of the two ways of seeing remain independent.

The phenomenal descriptions, obtained with the motion tests, suggest the necessity to distinguish between unity/oneness of an object and its heterogeneity/multiplicity as correlated to different ways of seeing. In fact, motion strengthens the phenomenal wholeness and oneness of the watercolored object even if multiple antinomic specific instances of it in different spatial or temporal locations can also be perceived at the same time. This happens without creating a visual paradox. These contradictions are only apparent and are due to their belongingness to different perceptual levels. The absence of switches between opposite figural statuses, i.e., from object to hole, and the inertia or resistance to variations of the perceived figural status are in favor of the necessity to introduce the notion of phenomenal wholeness as distinct from the phenomenal partialness.

4.1. What Does Wholeness Mean? Wholeness and Partialness

The need to introduce the notion of phenomenal wholeness and partialness is related to the basic problem of perceptual organization. Gestalt psychologists studied the perceptual organization in terms of grouping or figure–ground segregation. The grouping principles introduced by Wertheimer (1912a, b, 1923) described how individual elements create larger wholes separated from others and how the elements in the visual field ‘go together’ to form a holistic percept. The principles suggested by gestalt psychologists are unsuitable to describe appropriately the coexistence of the phenomenal wholeness and partialness. The notion of wholeness goes beyond the holistic percepts and larger wholes defined by the gestalt principles. In fact, the kind of whole defined, for example, by the similarity principle (Wertheimer, 1923) is an inner organization of elements that group together the most similar elements (in color, brightness, size, empty/filled, shapes, etc.) and, at the same time, segregate elements that are dissimilar. Each of the gestalt principles is a phenomenal/physical attribute grouping elements with similar specific properties and ungrouping elements with different attributes. Briefly, the gestalt principles behave like watershed.

The phenomenal wholeness, here introduced, suggests a more complex process, whose aim is to put together elements that not necessarily possess the same attribute and that can also be antinomic. Within the phenomenal wholeness single and different parts can be invisible by virtue of their belongingness to the whole, which presumes phenomenal assumptions of homogeneity, univocality and continuity without breaks or quantitative leaps. The phenomenal wholeness is a oneness process, through which many heterogeneous elements become one and a multiplicity becomes a unity. This is different from what is suggested by gestalt principles and it is different especially because the wholeness is complemented by an opposite party, which, by similitude, we suggest to call 'phenomenal partialness'. Just as the wholeness puts together different elements annulling their differences, the partialness breaks up or parcels out the elements of a whole underlining their individuality, difference, heterogeneity, discontinuity and multiplicity. The partialness is the reverse of the wholeness. Just as through the wholeness the single elements can become invisible, through the partialness the oneness can be invisible. Furthermore, the belongingness of the wholeness is replaced by the antagonism, separation and isolation of the partialness.

It is worth underlining that wholeness and partialness are two phenomenal processes in the sense that we clearly perceive both ways of organizing objects and parts. By being two ways of organizing they are also two opposite ways of seeing: the wholeness is like putting everything into the same basket or seeing the forest, the partialness is like seeing the trees and not the forest. What is invisible within the wholeness is visible within the partialness and *vice versa*. They complement each other and the visual system can easily switch from one process to the other as shown in the previous figures. This suggests that the two opposite phenomena are two complementary processes and depend on two complementary and opposite ways of seeing. The nature of these terms deserves to be more deeply studied.

4.2. How Artists Exploit Phenomenal Wholeness

Artists from ancient to modern times have struggled to understand how a few locally ambiguous contours or color patches on a flat surface can induce mental representations of a globally meaningful three-dimensional scene. Kandinsky's painting 'Autumn' (Fig. 8(a)) illustrates an understanding that conscious percepts of external reality are actively constructed by the visual brain. This painting carries out a

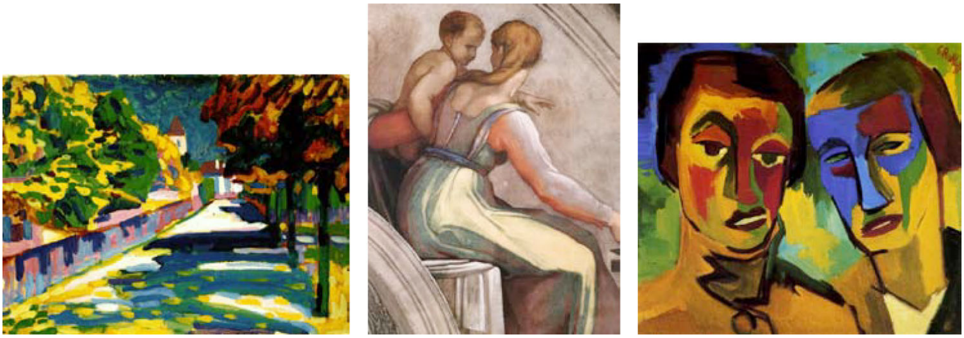

(a) (b) (c)

Figure 8. (a) A painting by Kandinsky, 'Autumn'. (b) Michelangelo's fresco. (c) A painting by Karl Schmidt-Rottluff. This figure is published in colour on http://brill.publisher.ingentaconnect.com/content/vsp/spv

bold break up of well-known forms, which tend to give way under the strokes of many different colors. Despite this fragmentation, for observers of this painting, «the landscape is clearly perceived within the mixture of colors» (100). «The forms are visible in spite of the splashes of colors» (100). «The colors define autumn in a little town» (91). «The figures emerge even if they are broken up or parceled out in many fragments or in many pieces of a chromatic mosaic» (98).

This painting shows something that is in-between part and whole. The parts emerge independently from the whole, but more importantly the whole can be perceived in spite of the mosaic of parts. This implies that the phenomenal wholeness makes it possible to perceive wholes despite multiple elements isolated and dissimilar. It also allows observers to see emerging objects like 'autumn' or reflexes of light through the brown leaves. Furthermore, the wholeness makes it easy to perceive the white road dotted with dry leaves and intersected by shadows of the trees. More specifically, the perception of the white road is perception of wholeness. If the shape of the road is clearly defined as a whole, its color is not, therefore it emerges as a consequence of the wholeness. A similar whole description can be used for the stone wall and the autumnal hill on the left side of the road. These emerging results cannot be explained with gestalt principles but only invoking a process that puts together different elements with different colors and properties.

Therefore the advantage of the phenomenal wholeness is to create oneness starting from a multiplicity and then to connect many elements in a single view and in a holistic singularity. A consequent advantage is that it discharges the multiplicity in favor of an emergent unity, e.g., autumn is the emergent unity, which discharges the multiple colors segregated or isolated by virtue of the gestalt principles and, by complement, puts together all the elements of the painting as a single thing. The title of the painting emphasized this phenomenal wholeness.

Another advantage is to make it difficult to perceive the multiplicity in favor of the oneness. In the fresco by Michelangelo, illustrated in Fig. 8(b), what is the color of the woman's dress? Is it green, red, blue, white? In this painting, Michelangelo used chromatic colors to fill the chiaroscuro gradient that helps to define the volumetric effect of the dress. Were achromatic shades of gray used instead, they would strengthen the wholeness of the dress. Instead, using different colors instead of different shades of gray weakens it, and made the amodal completion of color across the dress as a whole impossible (Pinna, in press). This makes it hard to identify the color of the woman's dress. The problem of the amodal completion of color emerges only after a question like 'what is the color of the dress?'. Before the question, this effect is not clearly noticed. As far as we know, no art historian reported this significant effect used so clearly by Michelangelo.

Even when the multiplicity of elements is visible like in the painting of Karl Schmidt-Rottluff (Fig. 8(c)), the phenomenal wholeness gives the visual system another advantage. In this painting, the coloration of the faces is broken up by the chromatic contrast of the large splashes of colors. However, they can be easily perceived and, more importantly, this chromatic contrast is perceived as something else, e.g., as part of an artistic style or expressing visual qualities, like pain, strangeness, etc. Therefore, the advantage is to discharge the multiplicity of contrasts and include them within new and more complex emerging properties, which cannot be otherwise visible. None of these emerging whole objects can be explained by invoking the gestalt principles.

The question is now: How does vision create phenomenal wholeness? A unified mechanistic answer to this question in terms of visual cortical architecture and dynamics may be found in the FACADE neural model of biological vision (Grossberg, 1994, 2003), as described in the next section.

5. How Does the Brain Perceptually Reconcile Watercolor Antimonies?

5.1. Boundary Grouping and Surface Filling-in

FACADE theory clarifies how the brain creates 3-D object representations through interactions of boundary grouping and surface filling-in processes within the cortical interblob and blob streams, respectively through cortical areas V1 through V4 (Grossberg, 1994, 1997); see Fig. 9. These boundary and surface processes exhibit computationally *complementary* properties (Grossberg, 2000) and their interactions generate a *consistent* perceptual representation that overcomes the complementary deficiencies of each stream acting on its own. These complementary properties include the following: Boundaries form *inwardly* between pairs or greater numbers of inducers, are *oriented*, and are *insensitive* to contrast polarity; that is, boundaries pool contrast information at each position from opposite contrast polarities.

Surfaces fill-in *outwardly* from individual lightness or color inducers in an *unoriented* fashion using a process that is *sensitive* to contrast polarity, which enables surfaces to embody visible colors and lightness percepts. These boundary and surface formation rules are obviously complementary.

How the brain selects and binds together a *consistent* percept from boundaries and surfaces that obey computationally *complementary* properties helps to explain

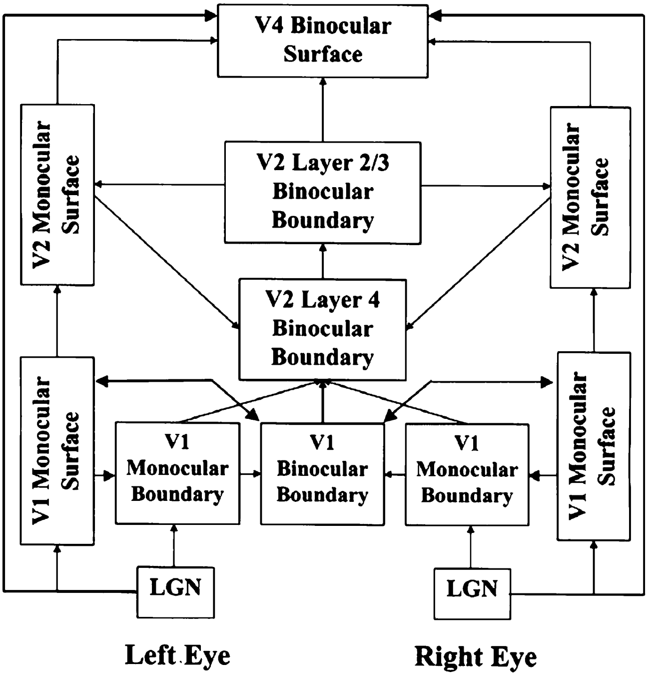


Figure 9. 3D LAMINART model macrocircuit. Feedback connections between boundaries and surfaces overcome the complementary deficiencies of each stream and lead to consistent conscious percepts. (Reprinted with permission from Fang and Grossberg (2009).)

many properties of perceptual wholeness. Thus, the 'wholeness' property of biological vision is mechanistically clarified within FACADE theory by the property of "complementary consistency" (Grossberg, 2008). Indeed, the fact that the brain achieves a *consistent* resolution of *complementary* tendencies clarifies, on the face of it, how perceptual *wholeness* can coexist with perceptual *antinomies*.

Boundary grouping and surface filling-in were first modeled by the Boundary Contour System (BCS) and Feature Contour System (FCS), respectively (Cohen and Grossberg, 1984; Grossberg, 1984; Grossberg and Mingolla, 1985; Grossberg and Todorovic, 1988). The word 'boundary' was introduced to emphasize that perceptual groupings can form in response to combinations of edge, texture, depth, and shading information, not merely edge information. This property is important when considering how the watercolor illusion and neon color spreading may be generated by combinations of dots as well as edges (Pinna and Grossberg, 2005).

A key early prediction, which has been increasingly supported by subsequent data, is that boundaries are *amodal* and do not, at least within the interblob cortical stream, carry visible lightness and color information. The amodal property of boundaries is due to their pooling of opposite contrast polarities at each position, which occurs no later than the complex cells of V1. This pooling operation enables boundaries to form around objects on textured backgrounds whose contrast relative to the object may reverse as the object boundary is traversed. The pooling process also allows the strongest possible boundaries to be formed using signals from all possible retinal detectors, both achromatic and chromatic. In particular, pooling to form a strong boundary clarifies how we can see continuous blue surfaces like the sea and sky (Grossberg, 1987a, Section 31; 1994, Section 37) even though blue cones on the retina are spatially very sparse (Boynton *et al.*, 1985; Brainard and Williams, 1993). Pooling of signals from opposite polarities and colors, however, prevents the boundary system from representing visible, or modal, visual features.

5.2. Broken or Weakened Boundaries in the Watercolor Illusion

Given that boundaries are amodal, how are visible surfaces seen? All visible lightness and color differences are predicted by FACADE to occur within the surface processing stream due to the filling-in of surface lightness and color, including the visible colors induced by the watercolor illusion. This hypothesis implies that, whenever surface colors are seen at locations far from their inducers, they must have spread there *via* surface filling-in. This property does not imply that boundaries are unimportant in the generation of visible surface qualities, since boundaries are predicted to both activate and serve as barriers to the surface filling-in process (Grossberg, 1994), including surfaces such as those caused by the blue cones mentioned above.

Boundaries can *activate* depth-selective surface filling-in when boundary and surface signals are aligned in space (Grossberg, 1994). Then depth-selective *surface capture* can occur whereby lightnesses and colors are seen on the correct surfaces in depth, such as during percepts of random dot stereograms (Fang and Grossberg, 2009), and unimodal or bistable percepts of transparency (Grossberg and Yazdanbakhsh, 2005) and the Necker cube (Grossberg and Swaminathan, 2004). In both kinds of bistable percepts, attention shifts can favor one percept over another. The current analysis also will predict how attention may play a role in resolving antinomies of perception.

Boundaries can also act as *barriers* to filling-in by gating, or inhibiting the spread of lightness or color, with the main effect that spreading lightness or color signals cannot freely cross a boundary. This gating hypothesis implies that, if surface lightness or color does manage to spread to positions beyond which they occur in a scene or image, then the boundaries which might otherwise have contained the spreading of this lightness or color must be broken or otherwise weakened to permit the leakage of lightness or color beyond them.

The present analysis extends the discussion in Pinna and Grossberg (2005) in which the FACADE model was used to provide a unified explanation of various watercolor illusion and neon color spreading properties. Indeed, the earliest neural network analysis of neon color spreading (Grossberg and Mingolla, 1985) critically used the spread of neon color to provide visible evidence for hypotheses about how boundary groupings are formed, and why these groupings might be broken or otherwise weakened at certain positions in response to neon color displays, thereby allowing neon color to spread beyond the locations of its scenic inducers.

5.3. Spatial Competition Weakens Boundaries in a Contrast-Sensitive Way

Typically, if a boundary is broken or weakened at a position where it might otherwise be expected to occur, this is due to some form of competition within the boundary system. Indeed, the BCS was, from the start, predicted to include both spatial and orientational competition networks in order to explain a wide range of data about perceptual grouping and filling-in of color and brightness (Grossberg, 1984; Grossberg and Mingolla, 1985). From a deeper perspective, these competitive interactions may be viewed as a kind of *hierarchical resolution of uncertainty* whereby the brain compensates for deficiencies in boundary detection at line ends and corners that arise from the very existence of oriented receptive fields. The main effect in the watercolor illusion can be explained by interactions between three properties: boundary strength is contrast-sensitive, nearby boundaries compete with each other *via* a process of spatial competition, and surface color can flow across positions where there are no boundaries or only weak boundaries.

As a result of boundary contrast sensitivity, stronger boundaries tend to form in response to the edges of higher-contrast colored lines than at lower contrast ones, so that stronger boundaries can inhibit nearby boundaries more than conversely, thereby enabling color to flow across these weakened boundaries. This interaction between boundary contrast, spatial competition, and boundary-gated surface filling-in provides an answer to the following questions: Why does a large luminance contrast difference between inducing lines show the strongest coloration effects? Why is there an asymmetry in the amount of color spreading from two inducing lines such that the color of the line with less luminance contrast relative to the background spreads proportionally more than the color of the line with more luminance contrast?

This happens in the BCS because the spatial competition is stronger from the boundaries of higher-contrast edges to those of lower-contrast edges than conversely; e.g., in Figs 1 and 2, the boundaries at the purple–orange and purple–white edges is stronger than the boundary of the orange–white edges. The boundaries of the lower-contrast edges are thus weakened more by competition than the boundaries of the higher-contrast edges. Hence more color can spread across these boundaries than conversely. In Figs 1 and 2, this explains the orange watercolor spreading throughout the figures. A similar idea was used to explain why neon color spreading is sensitive to the relative contrasts of the edges at which neon color is released (Grossberg and Mingolla, 1985a).

More recent modeling has clarified how perceptual boundaries are formed within the laminar circuits of visual cortex (Grossberg, 1999, 2003; Grossberg and Raizada, 2000; Grossberg and Swaminathan, 2004; Grossberg and Yazdanbakhsh, 2005; Grossberg *et al.* 1997; Raizada and Grossberg, 2001, 2003), and thereby showed how the predicted BCS operations are realized by identified cortical cell types and circuits. This LAMINART model (Fig. 10) explains and predicts a much larger set of data than was possible with the original BCS, including anatomical and neurophysiological data that support all the model's proposed cell and circuit properties. In particular, LAMINART predicts how spatial competition during boundary formation occurs between layers 6 and 4 of cortical areas V1 and V2, with longer-range grouping predicted to occur in V2 than V1.

The existence of spatial competition does not imply that the lower-contrast boundaries are entirely suppressed. If they were, then the color of the lower-contrast edge could not be distinguished from the watercolor that it causes. A key property of competitive and cooperative boundary interactions in the BCS and subsequent LAMINART models is that they preserve their analog sensitivity in response to the intensity of the inputs that drive them. This property, which is called *analog coherence*, has been shown through computer simulations to be robustly realized by the laminar circuits that carry out boundary grouping in cortical areas V1 and V2 (e.g., Grossberg and Raizada, 2000; Grossberg *et al.* 1997). This analog sensitivity depends on the fact that competition within the model uses on-center off-surround networks whose cells obey membrane equations with shunting dynamics. Such networks carry out contrast normalization through a divisive type of competition (Grossberg, 1973, 1980). These contrast-sensitive properties were used to define the oriented simple cells in the original Grossberg and Mingolla (1985a) explanation of neon color spreading properties and have subsequently been used to explain other cortical data, including data about simple cells, by many authors; e.g., Heeger (1992) and Douglas *et al.* (1995).

An implication of this competition hypothesis is that any boundary that can produce a similar weakening of a nearby, less contrastive, boundary at a colored region of prescribed size can cause a similar amount of color spreading from that region. In Figs 1 and 2, the main effect of boundary spatial competition is a local one whereby the more contrastive boundaries due to the purple lines inhibit the less contrastive boundaries due to the contiguous orange lines.

The watercolor illusion, as in Figs 1 and 2, derives its strength from the fact that a more contrastive and less contrastive edge are parallel to each another over a significant spatial extent. The total watercolor effect is derived from the cumulative effect of color leakage across the entire length of the weaker boundary and filling-in of the enclosed surface with the leaked colors. As a result, color leakage can occur across the entire length of the weaker boundary and spread its cumulative effects throughout the boundary-enclosed surface.

Such manipulations provide a way to test the spatial extent of the proposed competitive interactions. Earlier work has related the extent of spatial competition to other perceptual effects, such as neon color spreading, hyperacuity, texture segregation, persistence, binocular fusion and rivalry, and figure–ground separation (e.g., Francis *et al.*, 1994; Grossberg, 1987a, b; Grossberg and Mingolla, 1985; Grossberg *et al.*, 2008). This relationship predicts that there may be as yet experimentally unprobed connections between the spatial competitive effect in the watercolor illusion

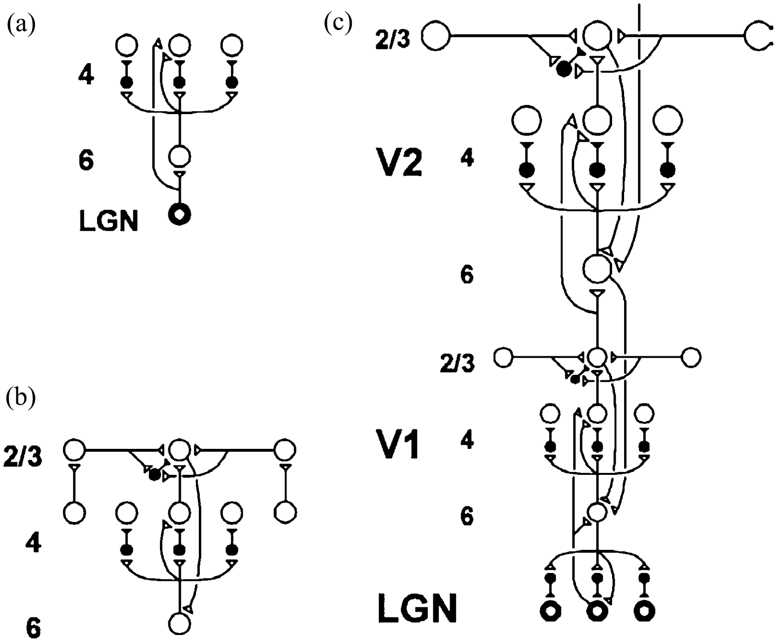


Figure 10. Some known cortical connections that are joined together and functionally explained in the LAMINART model of bottom-up, horizontal, and top-down interactions within visual cortical areas V1 and V2. See Raizada and Grossberg (2001) for summaries of supportive anatomical and neurophysiological data. Inhibitory interneurons are shown as filled-in black symbols. (a) The LGN provides bottom-up activation to layer 4 *via* two routes. First, it makes a strong connection directly into layer 4. Second, LGN axons send collaterals into layer 6 and thereby also activate layer 4 *via* the 6 → 4 on-center off-surround path. The combined effect of the bottom-up LGN pathways is to stimulate layer 4 *via* an on-center off-surround, which provides divisive contrast normalization of layer 4 cell responses. The excitatory and inhibitory layer 6 inputs to the layer 4 on-center are approximately balanced. As a result, the on-center receives a modulatory, but not driving, input. (b) Connecting the 6 → 4 on-center off-surround network to the layer 2/3 grouping circuit: like-oriented layer 4 simple cells with opposite contrast polarities compete (not shown) before generating half-wave rectified outputs that converge onto layer 2/3 complex cells in the column above them. Layer 2/3 contains long-range oriented recurrent connections to other layer 2/3 cells. A balance between excitation *via* long-range horizontal connections and short-range disynaptic inhibitory interneurons helps to control which layer 2/3 cells will fire, as does interlaminar feedback: layer 2/3 cells send activation to enhance their own positions in layer 4 *via* the 6 → 4 on-center and to suppress input to other layer 2/3 cells *via* the 6 → 4 off-surround. There exist direct layer 2/3 → 6 connections in macaque V1, as well as indirect routes *via* layer 5. (c) V2 repeats the laminar pattern of V1 circuitry but at a larger spatial scale. In particular, perceptual groupings form using the V2 horizontal layer 2/3 connections, which have a longer range than the connections in layer 2/3 of V1. V1 layer 2/3 projects up to V2 layers 6 and 4, just as LGN projects to layers 6 and 4 of V1. Higher cortical areas send attentional feedback into V2, which ultimately reaches layer 6, just as V2 feedback acts on layer 6 of V1. Feedback paths from higher cortical areas straight into V1 (not shown) can complement and enhance feedback from V2 into V1. Top-down attention can also modulate layer 2/3 pyramidal cells directly by activating both the pyramidal cells and the inhibitory interneurons in that layer. The inhibition tends to balance the excitation, leading to a modulatory effect. These top-down attentional pathways tend to synapse on apical dendrites in layer 1, which are not shown, for simplicity. (Reprinted with permission from Raizada and Grossberg (2001).)

and in these other types of phenomena. The role of spatial competition in helping to explain the perceptually important figure–ground effects in the watercolor illusion will next be discussed.

Spatial competition also clarifies the percept that emerges from Fig. 4. At the bottom of the figure, the purple lines have greater contrast at their purple–gray and purple–orange edges than does the orange–gray edge of the orange line. As a result, more orange color flows across the orange–gray edge inside the cross shapes. At the top of the figure, by contrast, the orange lines have higher contrast at their orange–black and orange–purple edges than does the purple–black edge of the purple line. As a result, more purple color flows across the purple–black edge into the star shapes.

5.4. Cooperative Boundary Groupings Contain Color Spreading

The competition effect is not sufficient to explain all aspects of the watercolor illusion. One basic additional property that must be explained is how the color that spreads from spatially discrete or continuous inducers can be contained within prescribed regions of space, whether the squares of Figs 1 and 2, or the cross and star shapes of Fig. 4. For these examples of the watercolor illusion, continuous closed boundaries exist whereby to contain the spreading color. For the amodal boundaries that form behind the green region in Fig. 3(f), there are no corresponding boundaries within the images themselves. The brain creates these boundaries using the process of perceptual grouping.

Perceptual grouping is the process whereby spatially distributed visual features become linked into object boundary representations. Sometimes groupings complete boundaries over positions that receive no contrastive inputs from an image or scene, as in the case of illusory contours. Although illusory contours are familiar examples of perceptual grouping, grouping also binds together contiguous perceptual boundary fragments, even complete straight lines that individually receive bottom-up sensory inputs, as in Figs 1, 2 and 4.

Boundary completion, including illusory contour formation, was predicted by the BCS to depend on a long-range oriented cooperation process whereby boundaries could form across image locations that receive no bottom-up contrastive signals (Grossberg, 1984; Grossberg and Mingolla, 1985). This cooperative process was predicted to obey a *bipole property* whereby the cooperating cells could fire, even if they received no direct bottom-up input, if they received (almost) colinear inputs with (almost) their preferred orientation from positions on both sides of their receptive field. Since these original predictions were made, neurophysiological, anatomical, developmental, and perceptual experiments have provided supportive evidence, and it has been possible to interpret both the competitive and the cooperative BCS mechanisms in terms of identified cells within the laminar circuits of cortical areas V1 and V2. Several recent articles review how this LAMINART model's cooperative and competitive feedforward and feedback mechanisms can be used to explain a large body of perceptual, anatomical, developmental and neurophysiological data; e.g., Grossberg (2003), Grossberg and Seitz (2003), Grossberg and Williamson (2001), and Raizada and Grossberg (2003).

For present purposes, the most important hypothesis is the following: The bipole property is predicted to be realized by cells in layer 2/3 of cortical area V2 that interact together *via* long-range horizontal connections (Fig. 10(b) and 10(c)). The spatial competition from layers 6 to 4 of V2 (Fig. 10(b) and 10(c)) directly influences the input strengths from layer 4 that activate the long-range horizontal connections in layer 2/3 of V2 that form perceptual boundaries. When the spatial competition weakens the activities of layer 4 cells, the perceptual boundaries in layer 2/3 that would otherwise form in response to these layer 4 inputs are correspondingly weakened. These weakened boundaries generate weakened barriers to filling-in within the filling-in domains of the surface cortical processing stream; e.g., the thin stripes of cortical area V2 (V2 Monocular Surface in Fig. 9) and their projections to V4 (V4 Binocular Surface in Fig. 9). As a result, discounted bottom-up color signals to these filling-in domains can spread, or fill in, more easily across these boundary positions.

5.5. Figure–Ground Separation in the Watercolor Illusion: Multiple-Scale Boundary Webs in 3-D Surface Capture

Why do the regions that fill-in with watercolor look like volumetric figures, while the regions abutting them look like holes, as in Figs 1–7? FACADE theory provides mechanistic neural explanations of this property of the watercolor illusion, among others. FACADE theory was originally introduced to qualitatively explain how the visual cortex generates 3-D percepts of objects separated in depth from their backgrounds (Grossberg, 1987, 1994). It was further developed to quantitatively explain and simulate many perceptual and neural data about 3-D vision, including data about the functional role of identified cell types within the laminar circuits of the visual cortex (Cao and Grossberg, 2005; Fang and Grossberg, 2009; Grossberg and Howe, 2003; Grossberg and McLoughlin, 1997; Grossberg and Swaminathan, 2004). A major insight from FACADE theory, and one that is particularly relevant to explaining properties of the watercolor illusion and perceptual wholeness, is how brain mechanisms that represent the 3-D world also respond to 2-D images with 3-D percepts whose figures are separated in depth from their backgrounds (Fang and Grossberg, 2009; Grossberg, 1997; Grossberg and Swaminathan, 2004; Grossberg and Yazdanbkhsh, 2005; Grossberg *et al.*, 2007; Kelly and Grossberg, 2000). These figure–ground mechanisms enable partially overlapping, occluding, and occluded image parts to be separated and completed in depth, as occurs in response to Figs 3(d)–(f) and 5–7.

In Fig. 1(a), for example, the watercolor illusion segregates the colored frame in depth and gives it the appearance of a rounded figural surface. In Fig. 1(b), the tilted square has this appearance. Several factors contribute to these percepts within FACADE theory. One factor is that there are depth-specific and color-specific networks within the surface stream wherein filling-in occurs. These networks are called filling-in domains, or FIDOs. FACADE theory predicts how depth-selective boundaries can selectively capture lightness and color signals to fill in a surface within a FIDO that represents the corresponding depth, but not at other depths. Surface filling-in within a particular FIDO is seen at a prescribed relative depth from the observer.

The determination of figure and background can be traced to how boundaries interact with surface inducers to selectively fill in FIDOs that represent different depths. In particular, when two colored lines of different contrast are contiguous, as with the purple and orange lines in Fig. 1, then three parallel rows of boundaries are generated at the white–purple, purple–orange, and orange–white edges. These boundaries are of progressively decreasing boundary strength. Such an array generates a spatially sparse version of a *boundary web*, or spatial array of boundaries that can restrict filling-in within relatively small surface regions. Earlier modeling studies predicted how a boundary web that is sensitive to a range of depths can elicit a percept of a rounded surface in depth (Grossberg, 1987a, b; Grossberg and Mingolla, 1987). This prediction was successfully tested in experiments using depth-from-texture images by Todd and Akerstrom (1987). In their data, the worst correlation between human psychophysical judgments of 3D shape from texture and model predictions was 0.985. More recently, Grossberg *et al.* (2007) have shown how multiple-scale boundary webs can quantitatively simulate both the data and the 3-D percepts generated by the Todd and Akerstrom (1987) experimental stimuli.

The main idea behind this predictive success can be summarized as follows, before it is applied to explain watercolor effect figural properties. Consider a 2-D shaded ellipse. How does such a 2-D image generate a percept of a 3-D curved surface? The 2-D image activates multiple filters, each sensitive to a different range of spatial scales (see the bottom-up pathways to layer 4 in Fig. 10(b) and 10(c)). Other things being equal, larger filters need bigger inputs to fire than do smaller filters. Likewise, larger filters can, other things being equal, binocularly fuse more binocularly disparate images, representing closer objects, than can smaller filters. Smaller filters can binocularly fuse only less binocularly disparate images and thus farther objects. In addition, larger filters can respond to a wider range of disparities than can smaller filters. As a result, an object at a given depth with respect to an observer can initially be represented by multiple spatial scales.

These disparity-selective properties of multiple-scale filters often go under the name of the *size-disparity correlation* (Julesz and Schumer, 1981; Richards and Kaye, 1974; Schor and Tyler, 1981; Schor and Wood, 1983; Schor *et al.*, 1984; Tyler, 1975, 1983). How does the brain decide which combination of multiple-scale filters will ultimately represent the depth of an object? The multiple-scale filters input to grouping cells, *via* layer 4-to-2/3 connections in cortical area V2, which use the cooperative and competitive interactions that are summarized above to select and complete boundary representations that are sensitive to different depths. These competitive interactions include the spatial competition that helps to explain how the watercolor effect occurs. The winning depth-selective boundaries selectively capture color inputs at FIDOs that fill in the captured color at the corresponding depth, while also bounding the regions within which the color can spread. If some of these boundaries are weakened, as in the contrast-sensitive spatial competition described above, then color can flow out of a region to the extent that the boundary has been weakened.

Now consider how multiple scales may respond to a shaded ellipse. Other things being equal, smaller scales can fire more easily nearer to the bounding edge of the ellipse. As the spatial gradient of shading becomes more gradual with distance from the bounding edge, it becomes harder for smaller scales to respond to this gradient. Thus, other things being equal, larger scales tend to respond more as the distance from the bounding edge increases. As a result, the regions nearer to the center of the ellipse look closer owing to the size-disparity correlation.

A similar thing happens, albeit with a more spatially discrete filter input, in response to a watercolor image such as the ones in Fig. 1. Here, just as in response to a shaded ellipse, there is a spatial array of successively weaker filter responses as the distance increases from the most contrastive edge of the display. These successively weaker filter responses activate boundary and surface processes much as one would expect from a spatially discrete version of a shaded ellipse, and these processes can generate a rounded appearance using the same size-disparity correlation mechanisms. A new property of the watercolor effect, which is due to the discrete changes in successive boundary contrasts, is that the spatially disjoint boundaries can weaken each other *via* spatial competition and thereby allow surface color to spread within the depth-selective boundaries that are formed in response to the multiple-scale filter responses. That is why the interior of the watercolor region can look a little closer to the observer than the bounding edge. Because of this perceived depth difference, a region suffused with the watercolor illusion can have a stronger figural quality than one filled with a uniform color, which tends to look flat, as in Fig. 3(d)–(f).

This combination of multiple-scale depth-selective cooperative–competitive boundary formation and surface filling-in mechanisms together explains the main properties seen in Fig. 2. As in the explanation of Fig. 1, the discrete boundary web that is induced by the watercolor borders enables the abutting locations of corresponding surfaces to fill in onto a nearer depth plane. By putting watercolor inducers on opposite sides of each square and frame in Fig. 2, the relative strengths of filling-in across each square or frame are weighed against the direct watercolor boundary web effects near purple–orange lines. As can be seen in Fig. 2, the spread of color can attenuate with distance from its inducers. When attention is focused on a region near a purple–orange line pair, its spatially local watercolor effect wins over color that has spread from a distant purple–orange line pair, so that the locally filled-in surface is seen as a nearer figure, whereas the more distally and weakly filled-in region is seen as a hole. More is said in Section 5.6 about how hole percepts are perceived.

A similar explanation clarifies how the percepts in Fig. 5 are created. As in Fig. 4, the progression from a light gray to a black background changes the relative contrasts of the orange and purple lines relative to their backgrounds. As a result, flipping orange and purple lines in front of the two different backgrounds in Fig. 5(b) creates a consistent boundary web structure across the square and the frame, one that favors figural status to the annulus between them, albeit induced on the left by the spread of orange and on the right by the spread of purple. Keeping the inducers consistent across the entire image in Fig. 5(a) causes a reversal in percept from a figure on the left to a hole on the right. The transparency that is seen in this percept is explained in Section 5.6 below.

5.6. Transparency in the Watercolor Illusion: T-junctions, End Gaps, Border Ownership, Holes and Amodal Completion

Figure 3(a) illustrates how the watercolor effect can create transparent percepts. In this transparent percept, the watercolor purple boundary intersects the vertical boundary at T-junctions. The top of the T belongs to the purple boundary, while its stem belongs to the occluded vertical boundary. In addition, the contrast of the watercolor purple boundary is greater than that of the vertical boundary, thereby creating a stronger boundary around the watercolor region. These two properties are enough to initiate a figure–ground separation process whereby the watercolor boundary can be seen in front of the vertical boundary.

This figure–ground separation process is initiated as follows, as illustrated in Fig. 11. The main idea is that, although the brain is sensitive to T-junctions in images and scenes, it does not need explicit T-junction operators to respond to them. Rather, basic properties of perceptual grouping *via* bipole cells already have this sensitivity. In Fig. 11(a), a black horizontal bar replaces the purple line and a gray vertical bar replaces the vertical line. The black bar forms a T-junction with the gray bar (Fig. 11(b)). The top of the T belongs to the occluding black bar, while the stem belongs to the occluded gray bar. Bipole long-range grouping (Fig. 11(c)) strengthens the horizontal boundary, while short-range competition weakens the vertical boundary (Fig. 11(d)). This creates a break in the vertical boundary that is called an *end gap*. End gaps enable the spread of color between the vertical gray bar and its background, and thereby initiate the process of separating the occluding black bar from the occluded gray bar in depth, leading to a percept in which the black bar appears in a slightly nearer depth plane than the gray bar. In addition, the shared boundary fragment between the black bar and the gray bar is captured by the watercolor boundary in a process called ‘border ownership’ (Bregman, 1981; Kanizsa, 1979; Nakayama *et al.*, 1989), thereby freeing the partially occluded vertical boundary from competition from the horizontal boundary, and enabling the partially occluded vertical boundary to be amodally completed behind the watercolor boundary. Applying these concepts to the image in Fig. 3(a) clarifies how the watercolor-inducing boundaries appear closer than the vertical boundary, and how the vertical boundary is amodally completed behind them.

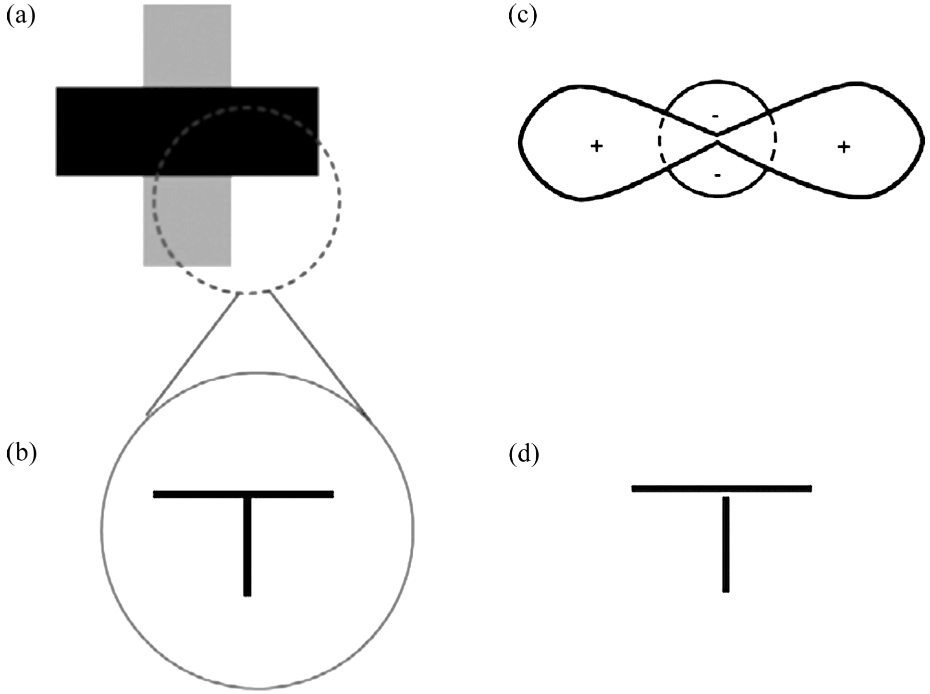


Figure 11. (a) In this 2-D picture, a dark horizontal bar is perceived to be in front of a gray vertical bar. (b) The local geometry of edges in the indicated area forms a T-junction. (c) In the form stream, the bipole combination of long-range cooperation (indicated by the Fig. 8) and short-range inhibition among nearby oriented units tuned to a variety of orientations (indicated by the circle) acts at the T-junction. Only the horizontal unit is shown. (d) The result of the cooperative–competitive dynamics in (c) is that the favored collinear structure of the horizontal edge wins at the top of the T, and a small *end gap* is created at the top of the stem of the T. Due to the way in which this boundary interacts with the surface formation stream, the top of the T is assigned to the Near depth, while the vertical segment is assigned to the Far depth. (Reprinted with permission from Berzhanskaya, Grossberg and Mingolla (2007).)

When the watercolor-inducing boundaries are segregated on a slightly nearer boundary representation than the amodally completed vertical boundaries, then each set of boundaries can activate surface filling-in within its respective depth-selective FIDOs. The watercolor boundary web further increases the percept of a depth separation. In the annular region between the two squares in Fig. 3(a), the orange watercolor spreads from the watercolor boundaries in front of two gray colors, which in turn spread from the vertical contrastive edge within their slightly farther FIDO. Due to this simultaneous perception of filled-in surfaces at the same positions but different depths, a transparent percept is perceived. See Grossberg and Yazdanbakhsh (2005) for quantitative explanations and simulations of unimodal and bistable transparency percepts that use these mechanisms. Also see Dresp *et al.* (2002) and Tse (2005) for experiments that support the FAÇADE prediction (Grossberg, 1994, 1997) about how end gaps initiate the separation of figures in depth.

However, a different percept, that of a hole, is perceived within the inner square of Fig. 3(a). This is because the boundaries of the purple and orange lines belong to a nearer depth plane, and the filling in cannot cross the purple boundaries into the inner square, or does it very little, when the orange–gray boundary contrast is much weaker than that of the purple–gray boundary contrast. As a result, the inner square is 'empty' at the nearer depth; that is, it is a 'hole'.

These figure–ground mechanisms also clarify the percepts in Fig. 3(b)–(e). Changing the contrast and color of the square does not alter the geometrical relationships that are defined by the T-junctions in these images. When the T-junctions are most salient, they can trigger figure–ground separation using the bipole grouping properties that are summarized in Fig. 11. In Fig. 3(c) and 3(d), for example, the T-junctions still help the watercolor frame to be represented on a nearer surface, which becomes even nearer still due to the watercolor boundary web. This latter factor helps the watercolor frame to look closer than the uniformly gray square, which thus continues to look like a hole relative to the watercolor frame, even though it appears in front of the vertical line that is amodally completed behind it. When the dark gray square is replaced by the green square in Fig. 3(e), a similar percept occurs.

Percepts of the inner square filled with dark gray (Fig. 3(d)) or green (Fig. 3(e)), however, bring into play other factors that can compete with the depth-separating boundary induction at the T-junctions. In particular, cooperative as well as competitive interactions between boundary *geometry* and *contrast* can reverse a relative depth percept (e.g., Dresp *et al.*, 2002; Grossberg, 1997, Fig. 4). Consider, for example, the black and gray rectangles in Fig. 11(a). Here boundary geometry and surface contrast factors *cooperate* to cause the long horizontal boundaries of the black rectangle to 'belong' to the black rectangle, and thus to be represented on a nearer depth plane than the partially occluded gray rectangle. In this case, bipole grouping cells can form stronger horizontal than vertical boundaries where the black and gray regions intersect. This is partly because, due to the T-junction geometry, the bipole cells that form the horizontal black boundaries get more geometrical support, where they intersect the vertical gray boundaries, than do the bipole cells that form the vertical gray boundaries themselves, which get most of their support from only one side. In addition to this geometrical factor, the contrast of the horizontal black–white boundary is greater than the contrast of the vertical gray–white boundary. Thus geometry and contrast both favor the horizontal boundary grouping in this case.

However, if the horizontal rectangle is light gray and the two vertical bars are black, then geometry and contrast *compete* against each other. As the luminance of the horizontal rectangle approaches that of the background, two black bars will be perceived in front of a uniform background, thereby reversing the relative depth percept.

In Fig. 3(d) and 3(e), the relative contrast of the purple–orange boundary can still be larger than that of the purple–gray or purple–green boundaries, thus still pushing the inner square into a hole percept. However, focusing attention on the inner dark gray or green squares, by increasing their relative effective contrast (Fazl *et al.*, 2009), can more easily enable them to be perceived as a figure that partially occludes the amodally completed vertical line. In addition, because green is represented on its own color-selective FIDO (Grossberg, 1994), that factor can also facilitate perceiving it as a ‘figure’ on the corresponding surface representation.

5.7. Stratification and Viewpoint-Dependence in the Watercolor Illusion

Figure 3(f) exploits the same mechanisms for amodal completion to generate an interesting variation in which the green square is seen in front of the oblique red bar. This figure also illustrates how spatial attention shifts can, by selectively amplifying T-junction or watercolor-inducing cues, lead to different percepts. Several recent modelling articles (e.g., Fazl *et al.*, 2009; Grossberg and Swaminathan, 2004; Grossberg and Yazdanbakhsh, 2005) explain and simulate how spatial attention can amplify both surface and boundary representations, and thereby shift the attended features into figures seen on a nearer depth plane.

When spatial attention is drawn to the T-junctions between the green square and the oblique red bar, the bipole depth-separation effect in Fig. 11(f) may be amplified and can become rate-limiting in making the green square look like a figure in front of the bar. In particular, the T-top of the square boundary activates cooperative bipole cells that have a grouping advantage over the T-stem boundaries that are activated by the red bar. The bar may then be seen behind the inner boundary of the watercolor region. When the eyes shift their gaze to the watercolor-inducing contours that surround the green square, however, then spatial attention amplifies those factors, so that the boundary web effects may become rate-limiting and lift the watercolor frame in front of the green square, which can then be perceived as a hole.

Paradoxically, the red bar also crosses in front of the watercolor region outer boundary at the upper right of the image. Its cooperative bipole cells therefore have the advantage there over those of the watercolor outer boundary. However, if one focuses attention on the watercolor-inducing boundaries, so that the square surface appears to be a hole within the watercolor surface, then the red bar can appear to be closer than the outer boundary of the watercolor region, yet farther than the watercolor region where it is occluded by, and therefore farther away, than the green square hole in the watercolor surface. This percept is a watercolor version of *Kanizsa stratification*, wherein also boundaries are perceived to be interleaved in depth due to similar grouping constraints (Grossberg, 1997; Kanizsa, 1985; Kelly and Grossberg, 2000). The watercolor illusion adds the nice additional feature of including a percept of transparency, albeit a paradoxical, view-dependent, one which dissolves when one’s gaze runs along each red bar.

The percepts induced by Fig. 6(a) and 6(b) have a similar explanation, with the additional feature that the T-junctions where the green vertical lines abut the watercolor inducers push the watercolor and hole percepts behind the depth plane at which the vertical green lines are perceived.

5.8. Wholeness, Complementary Consistency and Resonance

At least two distinct types of system-wide processes are predicted by the FACADE model to contribute to percepts of 'wholeness'. One concerns the property of 'complementary consistency' that was mentioned above. This property arises when feedback between the boundary and surface streams selects a consistent set of boundaries and surfaces that will be experienced as a unified percept. Feedback pathways between V1 boundaries and surfaces, and between V2 boundaries and surfaces, are shown in Fig. 9. An analysis of how these feedback processes work goes beyond the scope of the current work, although the feedback from V2 surfaces (V2 Monocular Surfaces in Fig. 9) to V2 boundaries (V2 Layer 2/3 Binocular Boundaries in Fig. 9) has already been used to explain how figure–ground separation is initiated, notably how boundaries of opaque occluding surfaces 'belong' to them and are perceived in front of the boundaries of the surfaces that they partially occlude. Functional roles of these feedback pathways and computer simulations that explain 3-D figure–ground percepts are found in several articles; e.g., Cao and Grossberg (2005), Fang and Grossberg (2009), Grossberg (1994, 1997), Kelly and Grossberg (2000).

Boundary–surface feedback generates a binding, or resonant, event through horizontal, or inter-stream, interactions across a similar level of cortical organization; e.g., within V1 or V2. A second type of system-wide feedback event that supports perceptual wholeness is a coordinated set of bottom-up/top-down resonances between multiple stages of the visual cortex and higher-level cortices, such as parietal cortex in the Where stream, and interotemporal cortex in the What stream. In particular, a surface–shroud resonance binds surface properties, say in cortical area V4, to a form-fitting distribution of spatial attention, say in posterior parietal cortex (Fazl *et al.*, 2009; Grossberg, 2009). Said intuitively, this resonance completes a surface representation and makes it coherent. This resonance focuses spatial attention upon an object surface. Such a surface–shroud resonance may be a necessary condition for consciously perceiving modal, or visible, surface percepts, and its absence may be one factor that contributes to the clinical condition of parietal neglect: see Fazl *et al.* (2009), Grossberg (2009), and Section 5.9 for further discussion.

A related kind of bottom-up/top-down resonance is a feature-prototype resonance that binds together distributed features in an object's prototype, say in V2 or V4, with the object category that links the features together, say in inferotemporal cortex. This kind of resonance focuses prototype (object) attention upon the attended features in an object.

Both types of resonances are linked in multiple ways. One key way is the boundary–surface resonance that achieves complementary consistency. As a result of such linkage, the entire visual system can resonate synchronously to create perceptual 'wholeness' and to thereby organize percepts of the paintings displayed in Fig. 8.

5.9. Watercolor Illusion During Motion

The percepts arising from inspection of Fig. 7 share much in common with those which arise from inspection of Fig. 5. In addition, the motion of the percept increases the unity of the percept within the entire watercolor contour, even if the relative contrast strengths of the orange–purple lines reverse as the figure moves from a white background to a black one, or conversely. The main new feature to explain is this persistence of a unitary percept and its resistance to change.

At least two factors contribute to this effect. The first factor concerns how any moving object attracts automatic attention due to the transients that it creates in a scene. Many psychophysicists have documented these effects, including Cavanagh *et al.* (2001), Pylyshyn and Storm (1988), and Yantis (1992) and neural models of motion perception explain how this may happen (Berzhanskaya *et al.*, 2007; Chey *et al.*, 1997; Grossberg *et al.*, 2001). These transients help to activate spatial attention regions such as posterior parietal cortex *via* the cortical Where processing stream through cortical areas V1, MT and MST. In parallel, parietal spatial representations also get activated by the moving surface representations that are computed in the cortical What processing stream through cortical areas V1, V2 and V4. The activated parietal region sends depth-selective positive feedback signals to its generative surface representation in V4. This positive feedback cycles between the surface and spatial attention regions to generate a form-fitting locus of spatial attention, also called an *attentional shroud* (Tyler and Kontsevich, 1995) in the parietal cortex that is bound to its surface representation (Fazl *et al.*, 2009). As noted in Section 5.8, this bound state is called a *surface–shroud resonance*. Because of this positive feedback loop, a surface–shroud resonance has properties of persistence that enable a representation to resist momentary changes in input conditions. Because of the depth-selectivity of a surface–shroud resonance, it will tend to preserve the relative figure and hole relationships that existed when the surface–shroud resonance is initiated.

Fazl *et al.* (2009) have predicted that such a surface–shroud resonance plays a key role in enabling the brain to associate different view categories of an object to an emerging view-invariant object category, as the object moves with respect to an observer. It remains to be seen if watercolor illusion demonstrations can be used to further test this prediction.

Acknowledgements

Partially supported by CELEST, a National Science Foundation Science of Learning Center [SBE-0354378] and the SyNAPSE program of the Defense Advanced Research Project Agency [HR0011-09-C-0001] (to S. Grossberg). Supported by Finanziamento della Regione Autonoma della Sardegna, ai sensi della L.R. 7 agosto

2007, n. 7 (to M. Tanca and B. Pinna); Fondo d'Ateneo (ex 60%) and Alexander von Humboldt Foundation (to B. Pinna).

References

Berzhanskaya, J., Grossberg, S. and Mingolla, E. (2007). Laminar cortical dynamics of visual form and motion interactions during coherent object motion perception, *Spatial Vision* **20**, 337–395.

Boynton, R. M., Eskew, R. T. Jr. and Olson, D. X. (1985). Blue cones contribute to border distinctness, *Vision Research* **25**, 1349–1352.

Bozzi, P. (1975). Osservazioni su alcuni casi di trasparenza fenomenica realizzabili con figure a tratto, in: *Studies in Perception*, Flores-D'Arcais (Ed.), pp. 88–110. Giunti-Martello, Firenze, Italy.

Brainard, D. H. and Williams, D. R. (1993). Spatial reconstruction of signals from short-wavelength cones, *Vision Research* **33**, 105–116.

Brainard, D. H., Pelli, D. G. and Robson, T. (2002). Display characterization, in: *Encyclopedia of Imaging Science and Technology*, J. Hornak (Ed.), pp. 172–188. John Wiley & Sons Inc., New York, NY.

Bregman, A. L. (1981). Asking the 'what for' question in auditory perception, in: *Perceptual Organization*, M. Kubovy and J. R. Pomerantz (Eds), pp. 99–118. Lawrence Erlbaum Associates, Hillsdale, NJ, USA.

Cao, Y. and Grossberg, S. (2005). A laminar cortical model of stereopsis and 3D surface perception: closure and da Vinci stereopsis, *Spatial Vision* **18**, 515–578.

Cavanagh, P., Labianca, A. T. and Thornton, I. M. (2001). Attention-based visual routines: sprites, *Cognition* **80**, 47–60.

Chey, J., Grossberg, S. and Mingolla, M. (1997). Neural dynamics of motion grouping: from aperture ambiguity to object speed and direction, *J. Optic. Soc. Amer.* **14**, 2570–2594.

Cohen, M. A. and Grossberg, S. (1984). Neural dynamics of brightness perception: features, boundaries, diffusion, and resonance, *Percept. Psychophys.* **36**, 428–456.

Douglas, R. J., Koch, C., Mahowald, M., Martin, K. A. C. and Suarez, H. H. (1995). Recurrent excitation in neocortical circuits, *Science* **269**, 981–985.

Dresp, B., Durand, S. and Grossberg, S. (2002). Depth perception from pairs of overlapping cues in pictorial displays, *Spatial Vision* **15**, 255–276.

Fang, L. and Grossberg, S. (2009). From stereogram to surface: how the brain sees the world in depth, *Spatial Vision* **22**, 45–82.

Fazl, A., Grossberg, S. and Mingolla, E. (2009). View-invariant object category learning, recognition, and search: how spatial and object attention are coordinated using surface-based attentional shrouds, *Cognit. Psychol.* **58**, 1–48.

Francis, G., Grossberg, S. and Mingolla, E. (1994). Cortical dynamics of feature binding and reset: control of visual persistence, *Vision Research* **34**, 1089–1104.

Grossberg, S. (1973). Contour enhancement, short-term memory, and constancies in reverberating neural networks, *Studies Appl. Math.* **52**, 213–257.

Grossberg, S. (1980). How does a brain build a cognitive code? *Psycholog. Rev.* **87**, 1–51.

Grossberg, S. (1984). Outline of a theory of brightness, color, and form perception, in: *Trends in Mathematical Psychology*, E. Degreef and J. van Buggenhaut (Eds), pp. 59–85. North-Holland, Amsterdam, The Netherlands.

Grossberg, S. (1987a). Cortical dynamics of three-dimensional form, color, and brightness perception, I: Monocular theory, *Percept. Psychophys.* **41**, 87–116.

Grossberg, S. (1987b). Cortical dynamics of three-dimensional form, color, and brightness perception, II: Binocular theory, *Percept. Psychophys.* **41**, 117–158.

Grossberg, S. (1994). 3-D vision and figure–ground separation by visual cortex, *Percept. Psychophys.* **55**, 48–120.

Grossberg, S. (1997). Cortical dynamics of three-dimensional figure–ground perception of two-dimensional pictures, *Psycholog. Rev.* **104**, 618–658.

Grossberg, S. (1999). How does the cerebral cortex work? Learning, attention, and grouping by the laminar circuits of visual cortex, *Spatial Vision* **12**, 163–185.

Grossberg, S. (2000). The complementary brain: unifying brain dynamics and modularity, *Trends Cognit. Sci.* **4**, 233–245.

Grossberg, S. (2003). How does the cerebral cortex work? Development, learning, attention, and 3D vision by laminar circuits of visual cortex, *Behav. Cognit. Neurosci. Rev.* **2**, 47–76.

Grossberg, S. (2008). The art of seeing and painting, *Spatial Vision* **21**, 463–486.

Grossberg, S. (2009). Cortical and subcortical predictive dynamics and learning during perception, cognition, emotion, and action, *Phil. Trans. Royal Soc. London* **364**, 1223–1234.

Grossberg, S. and Howe, P. D. L. (2003). A laminar cortical model of stereopsis and three-dimensional surface perception, *Vision Research* **43**, 801–829.

Grossberg, S. and McLoughlin, N. (1997). Cortical dynamics of 3-D surface perception: binocular and half-occluded scenic images, *Neural Networks* **10**, 1583–1605.

Grossberg, S. and Mingolla, E. (1985a). Neural dynamics of form perception: boundary completion, illusory figures, and neon color spreading, *Psycholog. Rev.* **92**, 173–211.

Grossberg, S. and Mingolla, E. (1985b). Neural dynamics of perceptual grouping: textures, boundaries, and emergent segmentations, *Percept. Psychophys.* **38**, 141–171.

Grossberg, S. and Mingolla, E. (1987). Neural dynamics of surface perception: boundary webs, illuminants, and shape-from-shading, *Computer Vision, Graphics, and Image Proc.* **37**, 116–165.

Grossberg, S. and Raizada, R. (2000). Contrast-sensitive perceptual grouping and object-based attention in the laminar circuits of primary visual cortex, *Vision Research* **40**, 1413–1432.

Grossberg, S. and Seitz, A. (2003). Laminar development of receptive fields, maps, and columns in visual cortex: the coordinating role of the subplate, *Cerebral Cortex* **13**, 852–863.

Grossberg, S. and Swaminathan, G. (2004). A laminar cortical model for 3D perception of slanted and curved surfaces and of 2D images: development, attention and bistability, *Vision Research* **44**, 1147–1187.

Grossberg, S. and Todorovic, D. (1988). Neural dynamics of 1-D and 2-D brightness perception: a unified model of classical and recent phenomena, *Percept. Psychophys.* **43**, 241–277.

Grossberg, G. and Williamson, J. R. (2001). A neural model of how horizontal and interlaminar connections of visual cortex develop into adult circuits that carry out perceptual grouping and learning, *Cerebral Cortex* **11**, 37–58.

Grossberg, S. and Yazdanbakhsh, A. (2005). Laminar cortical dynamics of 3D surface perception: stratification, transparency, and neon color spreading, *Vision Research* **45**, 1725–1743.

Grossberg, S., Mingolla, E. and Ross, W. D. (1997). Visual brain and visual perception: how does the cortex do perceptual grouping? *Trends Neurosci.* **20** 106–111.

Grossberg, S., Mingolla, E. and Viswanathan, L. (2001). Neural dynamics of motion integration and segmentation within and across apertures, *Vision Research* **41**, 2521–2553.

Grossberg, S., Kuhlmann, L. and Mingolla, E. (2007). A neural model of 3D shape-from-texture: multiple-scale filtering, boundary grouping, and surface filling-in, *Vision Research* **47**, 634–672.

Grossberg, S., Yazdanbakhsh, A., Cao, Y. and Swaminathan, G. (2008). How does binocular rivalry emerge from cortical mechanisms of 3-D vision? *Vision Research* **48**, 2232–2250.

Heeger, D. J. (1992). Normalization of cell responses in cat striate cortex, *Visual Neurosci.* **9**, 181–197.

Julesz, B. and Schumer, R. A. (1981). Early visual perception, *Ann. Rev. Psychol.* **32**, 575–627.

Kanizsa, G. (1979). *Organization in Vision: Essays on Gestalt Perception*. Praeger Press, New York, USA.

Kanizsa, G. (1985). Seeing and thinking, *Acta Psychologica* **59**, 23–33.

Kelly, F. J. and Grossberg, S. (2000). Neural dynamics of 3-D surface perception: figure–ground separation and lightness perception, *Percept. Psychophys.* **62**, 1596–1619.

Koffka, K. (1915). Zur Grundlegung der Wahrnehmungspsychologie. Eine Auseinandersrtzung mit Vittorio Benussi, *Zeitschrift für Psychologie* **73**, 11–90.

Kulikowski, J. J. (1978). Limit of single vision in stereopsis depends on contour sharpness, *Nature* **275**, 126–127.

Nakayama, K, Shimojo, S. and Silverman, G. H. (1989). Stereoscopic depth: its relation to image segmentation, grouping, and the recognition of occluded objects, *Perception* **18**, 55–68.

Pinna, B. (1987). Un effetto di colorazione, in: *Il laboratorio e la città*, V. Majer, M. Maeran and M. Santinello (Eds), p. 158. XXI Congresso degli Psicologi Italiani.

Pinna, B. (2005). The role of Gestalt principle of similarity in the watercolor illusion, *Spatial Vision* **18**, 185–207.

Pinna, B. (2008a). Watercolor illusion, *Scholarpedia* **3**, 5352.

Pinna, B. (2008b). A new perceptual problem: the amodal completion of color, *Visual Neurosci.* **25**, 415–422.

Pinna, B. (2010). What color is it? Modal and amodal completion of color in art, vision science and biology, *Intl J. Arts Technol.* **3**, 195–220.

Pinna, B. and Grossberg, S. (2005). The watercolor illusion and neon color spreading: a unified analysis of new cases and neural mechanisms, *JOSA A* **22**, 2207–2221.

Pinna, B. and Reeves, A. (2006). Lighting, backlighting and watercolor illusions and the laws of figurality, *Spatial Vision* **19**, 341–373.

Pinna, B. and Tanca, M. (2008). Perceptual organization reconsidered in the light of the watercolor illusion: the problem of perception of holes and the object–hole effect, *J. Vision* **8**, 1–15, http://journalofvision.org/8/7/8/, doi:10.1167/8.7.8

Pinna, B., Brelstaff, G. and Spillmann, L. (2001). Surface color from boundaries: a new 'watercolor' illusion, *Vision Research* **41**, 2669–2676.

Pinna, B., Spillmann, L. and Werner, J. S. (2003). Anomalous induction of brightness and surface qualities: a new illusion due to radial lines and chromatic rings, *Perception* **32**, 1289–1305.

Pylyshyn, Z. W. and Storm, R. W. (1988). Tracking multiple independent targets: evidence for a parallel tracking mechanism, *Spatial Vision* **3**, 179–197.

Raizada, R. and Grossberg, S. (2001). Context-sensitive binding by the laminar circuits of V1 and V2: a unified model of perceptual grouping, attention, and orientation contrast, *Vis. Cogn.* **8**, 431–466.

Raizada, R. and Grossberg, S. (2003). Towards a theory of the laminar architecture of cerebral cortex: computational clues from the visual system, *Cerebral Cortex* **13**, 100–113.

Richards, W. A. and Kaye, M. G. (1974). Local *versus* global stereopsis: two mechanisms? *Vision Research* **14**, 1345–1347.

Rubin, E. (1915). *Synsoplevede Figurer*. Kobenhavn, Glydendalske, Denmark.

Rubin, E. (1921). *Visuell Wahrgenommene Figuren*. Kobenhavn, Gyldendalske Boghandel, Denmark.

Schor, C. M. and Tyler, C. W. (1981). Spatio-temporal properties of Panam's fusional area, *Vision Research* **21**, 683–692.

Schor, C. M. and Wood, I. (1983). Disparity range for local stereopsis as a function of luminance spatial frequency, *Vision Research* **23**, 1649–1654.

Schor, C. M., Wood, I. and Ogawa, J. (1984). Binocular sensory fusion is limited by spatial resolution, *Vision Research* **24**, 661–665.

Todd, J. T. and Akerstrom, R. A. (1987). Perception of three dimensional form from patterns of optical texture, *J. Exper. Psychol.: Human Percept. Perform.* **2**, 242–255.

Tse, P. (2005). Voluntary attention modulates the brightness of overlapping transparent surfaces, *Vision Research* **45**, 1095–1098.

Tyler, C. W. (1975). Spatial organization of binocular disparity sensitivity, *Vision Research* **15**, 583–590.

Tyler, C. W. (1983). Sensory processing of binocular disparity, in: *Basic and Clinical Aspects of Binocular Vergence Eye Movements*, C. M. Schor and K. J. Ciuffreda (Eds), pp. 199–295. Butterworth, Boston, MA, USA.

Tyler, C. W. and Kontsevich, L. L. (1995). Mechanisms of stereoscopic processing: stereoattention and surface perception in depth reconstruction, *Perception* **24**, 127–153.

Wertheimer, M. (1912a). Über das Denken der Naturvölker, *Zeitschrift für Psychologie* **60**, 321–378.

Wertheimer, M. (1912b). Untersuchungen über das Sehen von Bewegung, *Zeitschrift für Psychologie* **61**, 161–265.

Wertheimer, M. (1922). Untersuchungen zur Lehre von der Gestalt. I, *Psychologische Forschung* **1**, 47–58.

Wertheimer, M. (1923). Untersuchungen zur Lehre von der Gestalt. II, *Psychologische Forschung* **4**, 301–350.

Yantis, S. (1992). Multielement visual tracking: attention and perceptual organization, *Cognit. Psychol.* **24**, 295–340.