CHAPTER 5

From perceptive fields to Gestalt

Lothar Spillmann*

Dept. of Neurology, Neurozentrum, University Hospital, Breisacher Strasse 64, 79106 Freiburg, Germany

Abstract: Studies on visual psychophysics and perception conducted in the Freiburg psychophysics laboratory during the last 35 years are reviewed. Many of these were inspired by single-cell neurophysiology in cat and monkey. The aim was to correlate perceptual phenomena and their effects to possible neuronal mechanisms from retina to visual cortex and beyond. Topics discussed include perceptive field organization, figure-ground segregation and grouping, fading and filling-in, and long-range color interaction. While some of these studies succeeded in linking perception to neuronal response patterns, others require further investigation. The task of probing the human brain with perceptual phenomena continues to be a challenge for the future.

Keywords: perceptive fields; gestalt; neurophysiological correlates of perception; visual illusions; figure-ground segregation and grouping; fading and filling-in; long-range color interaction

When I was a student, Gestalt factors were hardly more than a set of phenomenological rules to describe figure-ground segregation and grouping. Nowadays, Gestalt factors have entered the fields of neurophysiology and neurocomputation (Spillmann and Ehrenstein, 1996, 2004; Ehrenstein et al., 2003). Rüdiger von der Heydt is studying them, Steve Grossberg incorporates them into his models, and Wolf Singer refers to them within the context of synchronization of oscillations. The common goal is to promote an understanding of Gestalt factors in terms of specified single-neuron activities and to find the neuronal correlates of perceptual organization.

In his 1923 classical paper, the founder of Gestalt psychology, Max Wertheimer, had proposed that what we see is the simplest, most balanced, and regular organization possible under the circumstances. He called this the Prägnanz principle and attributed it to the tendency of the brain towards equilibrium. Gestalten are distinguished by two main criteria:

(i) Supra-additivity, meaning that the whole is different from the sum of its parts. Michael Kubovy would call this a preservative emergent property, because the elements survive, while something new emerges.

(ii) Transposition, implying that a Gestalt maintains its perceptual properties regardless of figural transformations (e.g., distance, orientation, slant). This constancy is nowadays called viewpoint invariance.

The Gestalt approach challenged the view that vision can be understood from an analysis of stimulus elements. Instead, it proposed Gestalt factors according to which stimulus patterns are segregated into figure and ground and individual parts grouped into a whole. Gestalt factors include proximity, similarity, symmetry, smooth continuation, closure, and common fate and are described within the framework of “good Gestalt” or Prägnanz. Little was known at the time about the neuronal mechanisms underlying these factors.

*Corresponding author. Tel.: +49-761-270-5042; E-mail: lothar.spillmann@zfz-brain.uni-freiburg.de

DOI: 10.1016/S0079-6123(06)55005-8 67
Recent psychophysical and neurophysiological studies have shed light on some of the processes that may be responsible for figure-ground segregation and grouping (Valberg and Lee, 1991; Spillmann, 1999). The filling-in of gaps by illusory contours, the formation of boundaries by texture contrast, and the binding by coherent motion are among the better understood of these processes.

Part A. Atmosphere

Vision scientists who visited Freiburg from 1971 to 1994 may remember the building depicted in Fig. 1 (left), which housed our laboratory during those years. It was an old villa in one of the nicest neighborhoods in town, not far from the Schlossberg Mountain. When I arrived from America there was nothing in it, just empty rooms. So I found myself some old furniture and used equipment, a telephone, and dedicated collaborators. Ken Fuld, who had already worked with me in Boston, was the first. Billy Wooten followed from Brown, and then Charles Stromeyer and Bruno Breitmeyer from Stanford. Next were Arne Valberg and Svein Magnussen from Oslo. John S. Werner (UC Boulder), Munehira Akita (Kyoto), and Ted Sharpe (Cambridge) came later. Over the years, coworkers arrived from as many as 10 different countries, several of them returning for a second and third time. On the German side Wolfgang Kurtenbach and Christa Neumeyer, both zoologists, were among the first generation members. In 1994, we moved into the former Neurological Clinic (Fig. 1, right), just 200 m away, where we stayed for another 11 years.

From 1971 to 2005, the laboratory supported some 80 people at different stages of their careers, half of them diploma or doctoral students from biology, medicine, psychology, and physics. All of them were paid by grant money. Three former laboratory members moved on to become professors at German universities. Three visiting scientists were Alexander-von-Humboldt Senior Prize winners, nine were Humboldt Research Fellows, and five were supported by the German Academic Exchange Program (DAAD). Two Heisenberg Professorships were bestowed upon laboratory members. Even in our last year, we were fortunate to have a DFG-Mercator Guest Professor from the Netherlands. Altogether we published more than 200 research papers, 4 edited books, 1 book translation, 25 book chapters, and numerous conference contributions (http://www.lothar-spillmann.de/). It is fair to say that Freiburg became a spot on the (perception) map.

Because of the great variety of people, there was also a great diversity of research. Guy Orban once remarked during a visit: “Lothar, I see everybody working on a different topic. You will never get famous this way.” He was right, but I always thought that people are best at what they like the best. So I let them do whatever they wanted.

Our villa was old, but cozy. It had been a physician’s residence and I kept as many of the permanent fixtures as possible. We had a kitchen, bathtubs, and even beds. We did experiments on the effect of vodka, grew marihuana on the balcony, and had wild and multilingual parties. Twice a year, we would go to the Kaiserstuhl and enjoy the local specialties — asparagus, pheasant, and venison. The atmosphere in the laboratory was very conducive to creative research. It was informal and relaxed, with much interaction, both scientific and social, among ourselves. The laboratory was very much the center of everybody’s life — not just a place to work.

While life in the laboratory was enjoyable, dealing with the University administration and the Medical faculty was not always easy. As a psychologist in a clinical setting, one had little status and virtually no power in the University hierarchy. To gain visibility and esteem we began organizing research seminars. Richard Jung, our director, once said: “When you can’t travel, you bring the world to your doorstep.” This is what we did, even though we traveled a lot. Professor Jung supported us generously and regularly attended our seminars. The Freiburg School of Neurophysiology (R. Jung, G. Baumgartner, O. Creutzfeldt, O.-J. Grüsser, and H.H. Kornhuber) had always attracted a good number of distinguished neurophysiologists from around the globe (for a historical review see Grüsser et al., 2005); now we added psychophysicists. There must have been some 300 such seminars.
over the years; many co-organized with Michael Bach from the local Eye Clinic. Much of what I know came from listening to those invited speakers.

Freiburg is a beautiful town surrounded by the Black Forest, the gastronomy is among the best in Germany, and there is plenty of good wine. Sometimes wine proved mightier than words. The first European Conference on Visual Perception in Marburg in 1978 (which then was called Workshop on Sensory and Perceptual Processes) also owes its success to this kind of currency. The last evening session was supposed to end at 10 p.m. The janitor wanted us out, but three bottles of Endinger Engelsberg sent him to his bed and we stayed on until long after midnight. This was the evening when the Dutch delegation under the leadership of Maarten Bouman (Fig. 2) and Dirk van Norren decided that the next meeting should be held in the Netherlands, and a tradition was born.

The Neurologische Klinik mit Abteilung für klinische Neurophysiologie in Freiburg (Fig. 1, right) was unique in Germany as it combined excellent clinical studies with first-rate basic research in human and animal subjects. The clinic was housed in a former sanatorium surrounded by a beautiful park. Every spare corner of the building was used for research and bustled with activity. Neurophysiological experiments on the visual, vestibular, somatosensory, and nociceptive sense modalities — and their multimodal interactions — were done.
next to oculomotor, EEG, and sleep recordings. A well-stocked library, two workshops for instrument development, and generous funding provided ideal conditions for productive research, resulting in many hundreds of publications.¹

To honor Richard Jung on the occasion of his 75th birthday, Jack Werner and I planned an international conference in Badenweiler. Progress was slow and in the summer of 1986, Professor Jung — while on a visit to Belgium — suffered a stroke and died. So we organized our conference in his memory and that of his friends and co-editors of the Handbook of Sensory Physiology — Donald M. MacKay (1922–1987) and Hans-Lukas Teuber (1916–1977). We were lucky: the German Research Council, the Airforce Office of Scientific Research, the Alexander von Humboldt-Foundation, and Heinz Wässle from the Max Planck Institute for Brain Research in Frankfurt supported us. In 1987, we took the participants to that wonderful old hotel, the Roemerbad, where at the turn of the 19th century Friedrich Nietzsche, Richard Wagner, and Anton Chekhov had lodged, and had a great time. Conference participants first interacted in small groups and then presented a given topic for plenary discussion, with no chair assigned to a session. To our surprise it worked.

The book on Visual Perception — The Neurophysiological Foundations (Eds. Spillmann and Werner, 1990) came out of the Badenweiler conference. The individual chapters were written by some of the finest scientists in the field, all writing in their own style. This prompted Brian Wandell to say in his review in Contemporary Psychology, “The book jumped into my lap like an excited puppy.” To judge from the number of sold copies (6500), the book appears to have served the vision community well. It is also one of the few that aimed primarily at correlating perceptual phenomena to their underlying neuronal mechanisms.

Phenomenology as a guide to brain research had always had a great tradition in Freiburg. Jung (1961, 1973) firmly believed that all percepts had physiological correlates. He had proposed B- and D-neurons for brightness and darkness perception even before they were called on- and off-neurons. He had read the writings of Purkinje, Mach, and Hering on subjective sensory physiology, and when I first arrived as a student in the spring of 1962, Hans Kornhuber asked me whether I wanted to do a doctoral thesis on the Hermann Grid illusion. The conference report on the Neurophysiology and Psychophysics of the Visual System (Eds. Jung and Kornhuber, 1961) had just appeared with a chapter by Baumgartner on the responses of neurons in the central visual system of the cat. In this chapter he presented his receptive, field model of the Hermann grid illusion (p. 309). To a young psychologist, the prospect of looking into the human brain without actually sticking an electrode into it was fascinating. This fascination has never left me throughout my entire life. In the following, I will describe some of the perceptual phenomena studied in our laboratory in conjunction with their possible neurophysiological correlates.

Part B. Science

Perceptive fields

Hermann grid illusion

The Hermann grid is characterized by the presence of dark illusory spots at the intersections of white bars. A physiological explanation of this illusion involves concentric center-surround receptive fields. A receptive field is the area on the retina from which the response of a ganglion cell or higher-level neuron can be modulated by light entering the eye. Take two on-center receptive fields, one superimposed on the intersection and one on the bar. While central excitation is the same for both, the receptive field on the intersection receives more lateral inhibition than the receptive field on the bar (Fig. 3A). As a result the intersection looks darker. On a black grid, the intersections look lighter due to less lateral activation in off-center fields.

To test his hypothesis, Baumgartner and collaborators (Schepelmann et al., 1967) recorded from neurons in the cat visual cortex and found

that each bar presented by itself on the receptive field of the neuron produced a strong response (Fig. 3B). However, when both bars were presented together as in the intersection of the grid, the neuronal response was greatly reduced. Baumgartner postulated that the illusion should be strongest when the width of the bar matched the receptive field center (Tom Troscianko would later say that a factor of 1.4 was more appropriate).

Here then was a psychophysical tool to study the receptive field organization in humans without invading the brain. All one needed to do was to find the grid that produced the strongest illusion. So I pasted a number of Hermann grids with different bar width on cardboard and presented them at various distances from the fixation point. The task of the subject was to select the grid that yielded the darkest illusory spots.

Foveal field centers turned out to be quite small, only 4–5 min arc (Spillmann, 1971). However, with increasing eccentricity, center size increased up to 3° in the outer periphery (Fig. 4). The small center size in the fovea is the reason why the Hermann grid illusion is typically not seen with direct fixation. The bars are just too wide (Baumgartner, 1960, 1961).

Jung called these centers perceptive field centers because they are revealed through our perception

![Fig. 3. Hermann grid illusion. (A) Dark illusory spots are attributed to more lateral inhibition of neurons whose receptive fields are stimulated by an intersection as compared to a bar. (B) Single-cell recording from first-order B-neuron in the cortex of the cat with one or two bars stimulating the receptive field. The firing rate is reduced when both bars are presented simultaneously, consistent with a darkening at the intersection. (Modified from Baumgartner, 1990, with kind permission from Springer.)](image)

![Fig. 4. Perceptive field center size derived from the bar width that elicited the maximum illusory effect in the Hermann grid illusion, plotted as a function of retinal eccentricity. Center size in the fovea is only 4–5 min of arc, which is the reason why the dark illusory spots are normally not seen in foveal vision. (Modified from Jung and Spillmann (1970), with kind permission from the National Academy of Sciences of the United States of America.)](image)

(Jung and Spillmann, 1970). You may argue that a perceptive field reflects the activity of many neurons, not just one. This is undoubtedly true. Moreover, we do not know where these neurons reside in the visual pathway. So, it is difficult to
assign a given percept to the retina, lateral geniculate body, or visual cortex.

However, there are ways to narrow down the possible brain loci. For example, if the Hermann grid illusion cannot be seen with dichoptic presentation, we would say that it is most likely of subcortical origin. On the other hand, if it exhibits a strong oblique effect, we would assume that it is cortical. Finally, if the illusion can be seen with isoluminant colors, it is likely mediated by the parvocellular pathway. All three statements apply to the Hermann grid illusion. We therefore tend to think that it is primarily a retinal effect with a cortical contribution (for a review see Spillmann, 1994).

As did Colin Blakemore, we call these and other techniques the psychologist's microelectrode (a term variously attributed to Bela Julesz, John Mollon, and John Frisby) because of the insights they can provide into the mechanisms of visual perception and their location in the visual pathway. Peter Schiller's (Schiller and Carvey, 2005) recent paper in Perception proposes a new kind of cortical neuron to explain the Hermann grid illusion. Yet his proposal is still awaiting neurophysiological confirmation in the trained monkey.

When I went to America in 1964, I thought I would continue my Freiburg work studying visual illusions. Hans-Lukas Teuber (at MIT) was supportive, but David Hubel on the other side of the River was reluctant and recommended that I do straightforward neurophysiology. Torsten Wiesel was more sympathetic. It took Margaret Livingstone (Livingstone and Hubel, 1987; Livingstone, 2002) to bridge the gap between neurophysiology and perception at Harvard Medical School. Perceptual labels were boldly attached to visual structures and functions, and even illusions became fashionable among former hardcore neuroscientists.

**Phi-motion**

After measuring perceptive fields and field centers in the Hermann grid, we wondered whether we could also measure perceptive field centers for motion. The obvious choice was the phi-phenomenon. In 1912, Max Wertheimer (1912) had published his landmark study on apparent motion, which he attributed to some kind of intracortical short circuit (Querfunktionen). Our idea was simple: when two successively presented stimuli fell within the same perceptive field, there should be apparent motion; when they fell into different fields, there should be no interaction and — consequently — no motion.

So I measured the largest spatial distance over which phi-motion could be seen. The results are again plotted against retinal eccentricity; perceptive fields for motion were about 20 times larger than the perceptive field centers inferred from the Hermann grid illusion (Fig. 5). From this discrepancy we concluded that there were different kinds of perceptive field organization depending on the response criterium. This finding anticipated neurophysiological measurements that show receptive fields of area MT-neurons much larger than those

---

Fig. 5. Perceptive fields for apparent motion derived from the largest distance between two successively flashed stimuli across which phi-motion could still be seen, plotted as a function of retinal eccentricity. Regression lines refer to ascending and descending thresholds. Results obtained with the Hermann grid illusion are shown for comparison. (Modified from Jung and Spillmann, 1970), with kind permission from the National Academy of Sciences of the United States of America.)
of retinal ganglion cells or V1 neurons (Britten, 2004).

Westheimer paradigm

The 1960s and 1970s were the time of perceptual phenomena in search of neural mechanisms and neural mechanisms in search of perceptual phenomena. It was like a revelation; psychologists everywhere went wild. Colin Blakemore was the youthful leader of this group. Looking back, Baumgartner (1990) would later ask, "Where do visual signals become a perception?" The benefit was mutual; neurophysiologists looked for mechanisms that could not have been predicted from the physical stimulus alone. Vice versa, psychologists looked for percepts that may otherwise not have been discovered.

Naturally, we were not alone in our quest for psychophysical correlates of neuronal mechanisms. In 1965 and 1967, Gerald Westheimer (1965, 1967) published two influential papers in the *Journal of Physiology* on spatial interactions in the human retina (see also Westheimer, 2004). Westheimer used a small test spot centered on a variable background that in turn was superimposed on a large ambient field (Fig. 6A). With this kind of luminance hierarchy, he obtained the increment—threshold curve known as Westheimer function (Fig. 6B).

Threshold was plotted as a function of background diameter. When the background became larger, the threshold for the test spot first increased to a peak, then decreased, and finally leveled off. Westheimer attributed the initial increase to spatial summation within the perceptive field center (first arrow) and the subsequent decrease to lateral inhibition within the perceptive field surround (second arrow). In this way he derived the diameters of the center and the entire field.

I very much liked Westheimer’s paradigm. So I asked Anne Ransom-Hogg (Ransom-Hogg and Spillmann, 1980), now Anne Kurtenbach, in my laboratory to measure perceptive fields and field centers in the light- and dark-adapted eye. To do so, we used an elaborate three-channel Maxwellian-view system, beautifully crafted by our master technician. It had a swivel support (adopted from Billy Wooten’s laboratory), enabling us to do measurements out to 70° eccentricity without realigning the pupil. (We also had a four-channel Michelson interferometer, to which later were added two more Maxwellian-view systems, making our laboratory one of the best-equipped vision laboratories in Germany.)

With increasing retinal eccentricity, the position where the Westheimer curve peaked was displaced to the right, and so was the position of the point where the curve asymptoted. Therefore, when we plotted perceptive field center size as a function of eccentricity, both curves (for photopic and scotopic vision) increased from the fovea towards the periphery, just as for the Hermann grid illusion.
However, field centers were larger by approximately one fourth for scotopic than for photopic vision (Fig. 7). We attributed this difference to the peak shift caused by the decrease of lateral inhibition with dark adaptation and the resulting flattening of the curve. This finding agreed with Horace Barlow et al.’s (1957) discovery in the cat that at low-light levels the area for spatial summation increases when lateral inhibition gradually diminishes and disappears.

The study by Ransom-Hogg permitted a further conclusion. When we plotted perceptive field center size against the inverse of the cortical magnification factor (Drasdo, 1977), we obtained a straight line with a slope of 0.88. This finding suggested an almost constant size of the cortical representation of perceptive field centers; it also compared well with the slope of 0.81 found for cortical receptive field centers in the rhesus monkey (Hubel and Wiesel, 1974).

So far, we had tacitly assumed that the perceptive field organization in the human was similar to the receptive field organization in the monkey. But we had no evidence. Therefore, in a follow-up experiment, Regina Oehler (1985) in our laboratory used the Westheimer paradigm to measure perceptive fields and field centers in human and rhesus monkey. Fig. 8 shows her experimental setup.

The monkey and human curves were similar in shape and stacking order, but they differed in height (Fig. 9). However, when one derived the critical background diameters at which the curves peaked and leveled off, the resulting values were almost the same (Fig. 10). In fact, the match for perceptive field centers could not have been better. In comparison, perceptive field sizes were somewhat larger for the human observers, suggesting more extensive lateral inhibition.

After demonstrating that the perceptive field organization was equivalent in macaque monkeys and humans, the question remained: how do macaque perceptive field centers compare to macaque receptive field centers obtained neurophysiologically?

To answer this question we plotted the diameters of macaque perceptive field centers (obtained with the Westheimer paradigm) and receptive field centers of retinal ganglion cells (from DeMonasterio and Gouras, 1975) against eccentricity. Again, the agreement between the two kinds of measurements was excellent (Fig. 11).

Now we had evidence that perceptive field centers and receptive field centers in the monkey were equivalent. And what holds for the monkey should also apply to the human observer. So whenever we measure perceptive fields and field centers in man using the Hermann grid illusion, the Westheimer paradigm, or another procedure, we can safely say that we are tapping the underlying receptive field...
organization (of ganglion cells) without using a microelectrode (Spillmann et al., 1987).

**Beyond the classical receptive field**

So far I have described center-surround organization in classical receptive fields. This section addresses neurons whose response is modulated by stimulus properties from beyond the classically defined receptive field. Following the finding by McIlwayn (1964) that retinal ganglion cells respond to stimuli in the far periphery, Bruno Breitmeyer and Arne Valberg in our laboratory embarked on a series of studies to identify related psychophysical responses. They found that the increment threshold for a foveal stimulus increased in the presence of a grating shift as far as 4° away — the Jerk Effect (Breitmeyer and Valberg, 1979).

The neurophysiological breakthrough for long-range interactions came from the Zurich group of Günter Baumgartner (Baumgartner et al., 1984). Rüdiger von der Heydt and Esther Peterhans showed that the response rate of neurons could be affected by stimuli that were clearly outside the classical receptive field (von der Heydt et al., 1984; von der Heydt, 1987; von der Heydt and Peterhans, 1989). They called this the response field. This
discovery opened up the study of perceptual completion across gaps and scotomata, surface filling-in, large-scale color effects, and context-dependent boundary formation. Our review paper on this topic, 12 years later, was requested as often as 400 times (Spillmann and Werner, 1996).

In the stimulus pattern shown in Fig. 12 (left), one can perceive a bright vertical bar delineated by illusory contours. Von der Heydt and Peterhans studied this illusion neurophysiologically in visual area V2 (Fig. 12, right). They first presented a solid bar moving back and forth across the receptive field. The response was vigorous in each direction (A). Then they presented the same bar, but with a large gap in the middle, to spare the classical receptive field. Under these conditions, one would predict the neuron to fall silent, as there is nothing to drive the cell. However, this was not the case. Instead, the neuron continued to respond, albeit less strongly (B). This can only be explained by assuming that it received input from the two short bars at the top and bottom. Finally, when the bars were closed off with thin lines, the response was essentially absent (C). In this condition, the perception of the illusory contour also breaks down.

This finding had enormous consequences. It meant that we can perceptually recover an object that is only partially given by virtue of filling-in. It also opened the possibility of explaining a number of illusions that are characterized by perceptual occlusion, such as the Kanizsa triangle and the Ehrenstein illusion.

**Kanizsa triangle**

The Kanizsa (1979) triangle exhibits a triangular surface that is brighter than the surround and delineated by illusory contours (Fig. 13). Although the illusion is typically elicited by black solid cues (a), it will also arise from concentric rings (b), and even small dots at the apices (c). Illusory contours may be straight or curved depending on the shape of the missing sectors (d). Supporting lines jutting in from the side enhance the illusion.

Von der Heydt and Peterhans (1989) suggested that neurons responding to discontinuous bars also mediate the perception of the Kanizsa triangle illusion. According to their model (Fig. 14), end-stopped neurons in area V1, whose receptive fields are activated by the corners at the edges of the missing sectors, feed their signals into a gating mechanism in V2 neurons. Signals from two aligned sectors will be multiplied ($\times$) and then sent to a higher order neuron, where they will be summed with the input from the straight edges of the missing sectors ($\sum$). The result is an illusory line delineating the bright triangle across the interspace.

This model is consistent with the observation that the Kanizsa triangle only emerges when the three cut-out sectors (pacmen) are properly aligned. When they are rotated just by a small amount, the illusion weakens and disappears. This need for collinearity is an example of the Gestalt factor of good continuation. Meanwhile, it has been shown that mammals, birds, and even insects behave as though they perceive the Kanizsa triangle (Nieder, 2002). This clearly speaks for a bottom-up mechanism.
In the Ehrenstein (1954) brightness illusion, one perceives a bright disk in the center between the radial lines, delineated by an illusory ring that is orthogonal to the inducers (Fig. 15, left). This is known as line-end contrast. Ehrenstein pointed out that brightness enhancement disappears when a physical ring is superimposed onto the illusory contour. This observation suggests that one needs open gaps in order to have brightness enhancement. When the radial lines are laterally displaced or rotated out of alignment, the illusion becomes weaker and ultimately breaks down (for a review see Spillmann and Dresp, 1995). This again is evidence for the role of collinearity and the Gestalt factor of good continuation.

There is a fascinating property of the Ehrenstein illusion: the neon color effect (van Tuijl, 1975; for a review see Bressan et al., 1997). When a colored cross is used to connect the radial lines across the central gap, this region appears to be tinted with the color of the cross (Fig. 15, right). Christoph Redies (Redies and Spillmann, 1981; Redies, 1989) studied this effect in my laboratory and tentatively linked it to line-gap enhancement and end-stopped cells. Grossberg (“I like neon”) proposed a computational model that interprets neon color in terms of diffusion (Grossberg and Mingolla, 1985; Pinna and Grossberg, 2005). Another well-known illusion that shows how illusory contours are formed at right angles to the inducing line ends is the abutting grating illusion.
Fig. 13. Kanizsa triangle. The illusory triangle appears brighter than its surround and is delineated by an illusory edge. It also appears to lie slightly above the background. Various kinds of corner cues (a–d) elicit the same illusory percept. (Modified from Kanizsa, 1974, with kind permission from Il Mulino.)

Fig. 14. Kanizsa triangle with receptive fields (gray patches) of end-stopped cells superimposed onto the corners of the pacmen (left). The model (right) distinguishes between two neuronal paths: an edge-detecting path (black arrows) that receives its input from the aligned edges of the cut-out sectors; and a grouping path (gray arrows) that receives its input from the end-stopped neurons. The latter signals are fed into a V2 neuron where they are multiplied (×) and then sent to a higher order neuron, where they are summed with the input from the edge-detecting path (Σ). In this way, an illusory contour emerges at right angles to the inducing cues for which there is no physical equivalent. Receptive fields for the two paths are assumed to overlap on the same patch of retina. (Modified from Peterhans and von der Heydt, 1991, with kind permission from Elsevier.)
Abutting grating illusion

In the figure by Kanizsa (1974), a crisp line appears to run down the interface between two phase-shifted gratings (Fig. 16). Manuel Soriano et al. (1996) in my laboratory did a study on the abutting grating illusion and found that the illusory line depends crucially on the alignment of the tips of the horizontal lines along the same vertical. When the two gratings are slightly interleaved or pulled apart, the illusory line breaks down. For most stimulus parameters tested, such as number and spacing of lines, the psychophysical results paralleled the neurophysiological data obtained by Peterhans et al. (1986; Peterhans and von der Heydt, 1991) in the monkey.

These authors had demonstrated that an abutting grating line was almost as effective in eliciting a neuronal response as a real line (Fig. 12D). For an explanation, they suggested the same two-stage model as invoked for the Kanizsa triangle, except that in the abutting grating illusion, there are many more end-stopped neurons involved to support the illusory line between the two phase-shifted gratings.

Peterhans and von der Heydt (1989) also found neurons in area V2 of the monkey that may account for the high sensitivity of the illusory contour towards deviations from collinearity. They used a moving string of dots and found that for some cells a deviation of one of the dots by only 2 min arc from a straight line sufficed to offset the neuronal response. This finding points towards alignment detectors governing the perception of illusory contours according to the Gestalt factor of good continuation.

Figure-ground segregation

The Gestaltists already knew that a uniformly textured region would group together and become a surface. On the other hand, differences in texture would lead to segregation. The next section describes a study on figure-ground segregation by orientation contrast.

Orientation contrast

Victor Lamme (1995) asked whether a difference in orientation between the target and the background...
Fig. 17. Texture contrast by orientation (left). Neuron response in area V1 of the monkey (right). Boxes (a–d) illustrate schematically the stimulus relative to the background. The neuronal response is enhanced when the orientation of the target is orthogonal to that of the background. Note that the receptive field of the neuron (black rectangle) is entirely enclosed within the target (boundary not shown in the experiment). The difference in response must therefore be due to long-range interaction. (Modified from Lamme, 1995, with kind permission from the Society for Neuroscience.)

Fig. 18. Contour integration. (a) Aligned Gabor patches on a background of randomly oriented Gabor patches pop out perceptually when arranged as a semicircular curve, (b) but even more so when forming a complete circle. The number and overall distribution of Gabor patches is the same in both patterns, but the response of the brain is not. These percepts may be attributed to the Gestalt factors of good continuation and closure. (From Kovács and Julesz, 1993, with kind permission from the National Academy of Sciences of the United States of America.)
would affect the neuronal response, even if the receptive field of the neuron, onto which the target was superimposed, did not receive direct input from the surrounding background (Fig. 17). He found that when the orientation of the target was orthogonal to that of the background, the neuronal response was large (a) and (c). However, when the orientation of the target was the same as that of the background, the response was small (b) and (d). The difference in response between the two conditions suggested that the background had an effect on the target response through long-range interactions. This experiment shows that figure-ground segregation by orientation contrast can occur as early as area V1 (see also Lamme et al., 1992). In the cat, responses to motion contrast have also been found in striate cortex (Kastner et al., 1999).

Contour integration
While alignment plays a role in illusory contour formation, it is also essential for perceptual grouping. I had first seen chains of aligned Gabor patches in Robert Hess’s laboratory in Montreal (Field et al., 1993), but at the time did not appreciate their importance for contour integration. Fig. 18 is from the work of Kovács and Julesz (1993). It shows an assembly of Gabor patches with different orientations. Within this pattern, there are six patches that line up to form a curvilinear contour (a). This is an example of the Gestalt factor of good continuation. However, the curved contour pops out much more easily when the ring is complete (b). This is an example of the Gestalt factor of closure. Obviously, the neuronal mechanism underlying this kind of contour integration must be effective over a rather large distance; otherwise, there would be no grouping (Spillmann and Werner, 1996).

Grouping by coherent motion
In the domain of motion, the Gestalt factor of common fate is probably the most important of all. This factor implies that coherently moving dots on a background of randomly moving dots will pop out as a group, even if the dots are fairly widely spaced.

Bill Uttal and Allison Sekuler (Uttal et al., 2000), both guest researchers in my laboratory, asked: How common must common fate be? They found that only 4 coherently moving dots, within a dynamic noise background of 100 dots, were sufficient in order to be seen as a group (Fig. 19). This is a very low signal-to-noise ratio. Frank Stürzel (Stürzel and Spillmann, 2004) further found that the time needed for grouping is only 430 ms. He also showed that coherent motion obeyed several of the constraints known from neurophysiological studies, such as speed and angular deviation from parallel trajectories. Finally, Gunnar Johansson’s (1973) biological motion stimuli demonstrated that grouping by common fate occurs even when individual dots have different motion vectors.

Is there a neurophysiological correlate to support these psychophysical observations? The answer is yes. In a carefully designed experiment, Britten et al. (1992) showed that neurons in primate area MT respond strongly to coherently moving dots. Furthermore, they demonstrated that the neuronal threshold was comparable to the behavioral threshold measured simultaneously in the same animal. Neuroimaging in the human has confirmed area V5 as the brain locus responsible for mediating perception of motion coherence.

Fig. 19. Coherent motion. Four aligned dots moving in the same direction and at the same speed group perceptually together on a background of randomly moving dots. All dots were white on a black background. Parallel trajectories facilitate grouping, but are not necessary. This is an example of the Gestalt factor of common fate. (Reprinted from Stürzel and Spillmann, 2004, with kind permission from Elsevier.)
Evidence from a recent study by Peterhans et al. (2005) further shows strong responses to rows of coherently moving dots already in macaque areas V2 and V3. These results demonstrate that the Gestalt factor of common fate is a basic mechanism of our neuronal inventory.

Many of the Gestalt factors mentioned can be found in the animal kingdom in the interest of camouflage. In his book, *Laws of Seeing*, Wolfgang Metzger (1936) showed that it is not just mammals that break figure-ground segmentation to hide from predators, but also insects, fishes and birds. The purpose is to blend in with the ground. Ramachandran et al. (1996) demonstrated that a flounder displays on its skin the texture of a checkeredboard on which it is placed. This is amazing as it occurs within minutes. Hiding through camouflage is particularly effective when an animal “freezes,” although in a moving environment the absence of motion will likely reveal an animal.

Metzger argued that if predators get fooled by camouflage much in the same way as we do, their visual systems must be processing information in a way similar to ours. He therefore considered the Gestalt factors to be both innate and bottom-up. However, the early Gestaltists already knew that there were also top-down effects such as attention, set, motivation, and memory. Neurophysiologists, especially Mountcastle (1998) and Schiller (1998), have actively investigated the feedback loops, including guided eye movements, required for top-down modulation. It is now clear that visual perception uses both bottom-up and top-down processes.

**Fading and filling-in**

*Troxler effect*

The previous sections emphasized the spatial aspects of the perceptive field organization and grouping. This section will address the temporal aspects. Here we asked how a surface is sustained over time. Stuart Anstis’ chapter in this volume mentions some of our earlier studies on the Troxler effect using static, rotating, and flickering targets. Christa Neumeyer in our laboratory was the first to study fading of large, centrally fixated disks (Neumeyer and Spillmann, 1977). She used various figure-ground contrasts and found that figures typically fade into the ground, not vice versa. Furthermore, when an oscillating grating surrounded the target, fading time was shorter. This observation is consistent with a later finding that a kinetic contour facilitates fading, rather than delaying it (Spillmann and Kurtenbach, 1992).

Research into fading picked up with the beautiful effects on color and texture filling-in demonstrated by Ramachandran and Gregory (1991). These findings involved grating patterns and page print, suggesting a postretinal origin. A few years later, Peter DeWeerd et al. (1995) showed neurophysiologically that texture fading occurred in area V3 of the visual cortex.

DeWeerd used a pattern with a white square on a dynamic background of vertical slashes (Fig. 20, top). The white target is called an *artificial scotoma* in analogy to a real scotoma. To make this target disappear, fixate at the small disk in the upper left corner for about 15 s. While fixating, you will see that the white target area becomes less distinct and eventually fades into the background. This is an example of texture spreading or filling-in. DeWeerd distinguished between two processes: a slow process for breaking down the border (cancellation) and a fast process for filling-in properties from the surround (substitution).

In Fig. 20 (bottom), the response rate of a V3 neuron in the monkey is plotted as a function of time. The continuous curve (hole) shows the response when the white target was present over the receptive field and the dotted curve the response when there was no hole in the background. The continuous curve first decreases, then gradually increases, and finally approaches the upper control curve. The interesting aspect here is that the firing rate for the “hole” condition recovers over time, although there is no change in the stimulus.

DeWeerd interpreted this “climbing activity” as the neuronal correlate of fading. When the two curves merged, the neuron could no longer distinguish between the two types of stimuli. He then asked human observers to look at the same pattern with steady fixation and report when the white target had faded into the background. The time needed for perceptual completion was quite similar
to the time required for neuronal completion (shaded area). When a red square was used for a target, fading time increased. This suggests an effect of stimulus salience.

Texture fading
Ralf Teichmann in our laboratory studied the effect of salience on fading time, systematically (Teichmann and Spillmann, 1997). He presented a striped target disk within a grating background and varied the difference in angle between the target and the background (Fig. 21). Fading time was longest when target and background were oriented approximately orthogonally to each other, i.e., when the target was most salient.

Catherine Hindi Attar has recently taken this approach one step further. She used two patterns by Giovanni Vicario (1998), a randomly oriented center within a uniformly oriented surround (Fig. 22, left)
and its converse, a uniformly oriented center within a randomly oriented surround (Fig. 22, right). Although the two patterns are made up from the same textures, they do not have the same perceptual salience. The center with the randomly oriented bars stands out much more clearly than its converse, and it takes several seconds longer to fade. This may be because this type of texture activates many orientation channels, thereby producing a stronger neuronal response than a uniform texture. (For a review see Spillmann and DeWeerd, 2003.)

**Filling-in of the blind spot**

While filling-in of an artificial scotoma requires a trained observer and good fixation, filling-in over the area of the blind spot is effortless and immediate (Ramachandran and Gregory, 1991). This is because in the first case, the hole is in the physical stimulus and must first be adapted to before it is filled-in with the color and pattern of the surround. In the case of the blind spot, however, the hole is on the retina and it has been there since birth. It is therefore not surprising that nature has provided us with a mechanism that replaces the hole with the stimulus properties of the surround without our doing. There are no photoreceptors in the retinal area corresponding to the blind spot and therefore no signals from there reach the brain. Nevertheless, we do not normally notice the blind spot. Even if we close one eye, we do not see it, although it is quite large (6° × 9°). We asked, how much information at the edge is needed to fill-in the blind spot?

We started by plotting the blind spot of my left eye. Once the blind spot had been charted, we presented a large red blob, somewhat larger than the blind spot (Fig. 23, top). It looked uniform—as it should. Then we cut out the center (Fig. 23, bottom). It still looked uniformly red. Finally, we reduced the width of the frame, making it narrower and narrower until it no longer became filled-in. In this way we arrived at a critical frame width of 6 arcmin for the minimum information necessary to fill-in the blind spot.

The same procedure was used for a textured background (stripes, dots). Here the critical width of the surrounding frame was about three times greater than for color, implying that more information was needed. However, uniform filling-in often was short-lived due to unstable fixation. Slight deviations of the eye from the fixation point resulted in partial...
filling-in, indicating that the frame was no longer spatially contiguous and in register to the border of the blind spot. To explain filling-in of the blind spot, we suggest a neuronal mechanism that detects the color at the edge and actively propagates it from there into the area of the blind spot (Spillmann et al., 2006).

Retinal scotomata
Next we asked whether acquired scotomata, such as those caused by a retinal lesion, also fill in. The answer is yes. Fig. 24 schematically presents a mechanism to account for filling-in. Neurons respond when light falls onto their receptive fields (left). However, when a patch of retina is destroyed by photoagulation, the deafferented neuron falls silent and, as a consequence, there will be a scotoma in the visual field. Surprisingly, the silence lasts only for a short while. Charles Gilbert (1992) has shown that only a few minutes after deafferentation a neuron in area V1 will begin to fire again when light falls onto the area surrounding the lesion (see also Spillmann and Werner, 1996).
One way to explain this reorganization is by collateral input activating the silenced neuron via horizontal fibers (thick arrows in Fig. 24, right). Such cortico-cortical connections are assumed to be functionally present all the time; however, in the case of local deafferentation, their influence may become potentiated owing to disinhibition. So one would expect that the receptive field of the neuron should become larger than it was before because of the inclusion of neighboring receptive fields. This is indeed the case. Gilbert found an enlargement of up to a factor 5. This enlargement may be responsible for the perceptual filling-in of the scotoma with stimulus properties from the surround. This enlargement may be responsible for the perceptual filling-in of the scotoma with stimulus properties from the surround. Gilbert found an enlargement of up to a factor 5. This enlargement may be responsible for the perceptual filling-in of the scotoma with stimulus properties from the surround. This enlargement may be responsible for the perceptual filling-in of the scotoma with stimulus properties from the surround.

I have asked a number of patients with diabetic retinopathy who had undergone retinal laser therapy how they perceived a uniformly white wall. If you consider that such patients have several hundred scars on their retinae, you would expect them to see a sieve with many dark holes in it. However, most of these patients said that their perception was largely unchanged. This is clear evidence for filling-in, although a control experiment using a textured wall remains to be done.

From perceptive field to Gestalt

Watercolor effect

How do we bridge the gap from perceptive fields to Gestalten? This is exemplified by the watercolor effect of Pinna et al. (2001, 2003). This effect is produced by a light-colored contour (e.g., orange) that runs alongside a darker chromatic contour (e.g., purple). In Fig. 25a, assimilative color (orange) is seen to spread from the chromatic double contour onto the enclosed surface area. The colored area is much larger than receptive fields of individual neurons. The watercolor effect may thus be thought of as an example of large-scale interaction from sparse stimulation, not unlike brightness and color perception on extended surfaces. Both percepts require transient edge signals and active propagation (i.e., filling-in) to sustain. Michael Paradiso (see his chapter in this volume) has presented psychophysical and neurophysiological evidence for such a mechanism.

We have shown that the watercolor effect exerts a strong effect on figure-ground organization. It thereby overrules the classical Gestalt factors such as proximity, good continuation, closure, symmetry, and Convexity (Fig. 25b). The asymmetric luminance profile of the stimulus defines what becomes figure and what ground. Invariably the side with the lower luminance contrast is seen as figure and that with the higher contrast as ground. By imparting illusory color the watercolor effect assigns unambiguous figure status to the perceptually tinted area.

This effect is consistent with Edgar Rubin’s (1915) notion that the border belongs to the figure, not the ground. A neurophysiological correlate of
border ownership may be sought in area V2 neurons that respond to an edge — such as black and white — in one direction, but not in the other (Zhou et al., 2000; Qiu and von der Heydt, 2005). Neurocomputational models of form perception assume that the outflow of color depends on a weakening of the boundary between differentially activated edge neurons through lateral inhibition. The resultant assimilative color spreads through the enclosed surface area until it is stopped by boundary contours on the other side (Pinna and Grossberg, 2005).

**Part C. Reminiscences and outlook**

The studies mentioned so far cover only a fraction of what we did in Freiburg. Of the numerous other experiments, I will only mention the research on rod-monochromacy. We were fortunate to have Knut Nordby from Oslo, a former student and colleague of Svein Magnussen’s (Fig. 26). Knut had no cones in his retinae, a very rare condition, making him an ideal subject for the study of rod vision.

Mark Greenlee and Svein Magnussen (Greenlee et al., 1988) looked at Knut’s spatial contrast sensitivity and orientation tuning and found that Knut had very low spatial frequency channels. They suggested that these had evolved by adapting to the lack of cones in his retinae. Arne Valberg says that he also had a much better contrast sensitivity, possibly due to reduced lateral inhibition.
For an account of his childhood and youth, see his autobiographic book chapter (Nordby, 1990).

Thereafter, Ted Sharpe (Sharpe and Nordby, 1990) in a series of sophisticated experiments looked at Knut’s vision from every angle. Some of the very best threshold curves in the literature came from this research, although Knut could not fixate. This testifies to his patience and dedication. Invitations from Cambridge and other prestigious laboratories followed. In the end he was the world’s best-researched rod monochromat. In 2004, we learned that Knut was very ill. Sadly, he died on April 25, of the following year.

There are a large number of experiments that I can only list by name: studies on Stiles’ $\pi$-mechanisms by Charles Stromeyer and Charles Sternheim; studies on the nature of brown by Ken Fuld, Jack Werner, and Billy Wooten; masking and metacontrast studies by Bruno Breitmeyer; studies on the tilt effect and tilt aftereffect by Svein Magnussen and Wolfgang Kurtenbach; and studies on the Abney effect by Wolfgang Kurtenbach; experiments on the so-called Ouchi illusion by myself (Spillmann et al., 1986) and the motion aftereffect by Nick Wade; a study by Holger Knau on the Ganzfeld; and studies on the persistence of moving arcs by Adam Geremek; a beautiful collaboration with Barbara Heider and Esther Peterhans from Zurich on stereoscopic illusory contours in man and monkey. Studies on S-cones by Keizo Shinomori and on the foveal blue scotoma by Svein Magnussen and Frank Stürzel were done in collaboration with Jack Werner in Sacramento. On a different topic, Mark Greenlee and Svein Magnussen together with Jim Thomas and Rolf Müller conducted a whole series of experiments on grating adaptation and short-term memory. There were clinically oriented studies by Walter Ehrenstein on interocular time thresholds in MS-patients, and by myself and Dieter Schmidt on partial recovery in prosopagnosia (patient WL). Lately we have also become interested in functional magnetic resonance imaging of the Pinna–Brelstaff illusion in collaboration with the Freiburg Department of Radiology. I think we have gone a long way.

Looking back, I guess I was lucky. I had excellent teachers: Wolfgang Metzger in Münster, Richard Jung in Freiburg, and Hans-Lukas Teuber in Cambridge, MA (Fig. 27). From them I learned much about Gestalt psychology, neurophysiology, and neuropsychology. In 1966, I entered Ernst Wolf’s laboratory in Boston, a German expatriate and utterly decent man, who introduced me to visual psychophysics, clinical testing of eye patients, and electrophysiology. I inherited from him my love for optical and mechanical apparatus and precise measurement. Ernst told me about Selig Hecht’s laboratory at Columbia and his early years at the Harvard laboratories of Comparative Zoology. Nobody knew his age, but he was as active, enthusiastic, and untiring as anyone. All these people taught me a lot, but — most importantly — they made me aware that we stand on the shoulders of others that paved the way. Sadly, most of our heroes and heroines from that time are no longer with

Fig. 27. Wolfgang Metzger (1899–1979), Richard Jung (1911–1986), and Hans-Lukas Teuber (1916–1976). (Sources unknown.)
us. But our admiration, respect, and affection for them continue.

It is the same with equipment. Who still remembers the cherished apparatus we used? Stimulus generators, oscilloscopes, Tektronix 602 displays, tachistoscopes, Maxwellian view systems? High-quality optics were necessary, precisely aligned components, stable light sources, IR and UV filters, prisms, collimators, achromatic lenses, first surface mirrors, narrow-band monochromators, electromagnetic shutters, neutral-density wedges, step filters, adjustable apertures, prisms, pellicles, and beamsplitters. All observations were done with subjects supporting themselves on a dentist-fitted, adjustable bite bar, so that the exit aperture was centered in the pupil. Highly sensitive radiophotometers were required for precise calibration. You had to be good with the soldering iron, too.

This is a bygone time. But I do remember how impressed I was when I visited Richard Gregory’s laboratory in Cambridge in the late 1960s. It looked more like a mechanics workshop than a vision lab: Helen Ross was sitting in a swing testing for size constancy. In Freiburg, individual spikes were counted from a filmstrip (sometimes using an abacus), Jerry Lettvin listened to neuronal spike activity simply by ear, and Hubel and Wiesel used a stick and a screen to find orientation-specific neurons in the cat. Baumgartner may have missed his chance because it took too long to build an apparatus for precise stimulus presentation (Jung, 1975). There should be a museum to keep these memories alive. A whole generation of expertise in building instrumentation for the life sciences seems to have gone lost. Nowadays, computers are much faster, more convenient, and powerful. Sometimes, I feel like a man from the Stone Age. But not everything can be done using a monitor.

Epilogue

May I end by saying: It was wonderful. We had all the freedom in the world to do what we wanted, where, when, and with whom. We have precious memories of the many guests and visitors who came to Freiburg. It is great to see the international vision community growing. National borders no longer play a role. The East has opened up, so that we see more and more representatives of those countries. In fact, the 2006 European Conference on Visual Perception will take place in St. Petersburg. Scientists are so much better than politicians at striking friendly relationships.

It is also rewarding to see that in Germany there are many more psychophysics laboratories now than there were in 1971, when we started. For 25 years I sent out information on jobs and positions to several hundred addresses via D-CVnet, to keep the German vision community together. Vision research is now actively pursued in Mainz, Frankfurt, Düsseldorf, Dortmund, Münster, Bremen, Kiel, Potsdam, Giessen, Tübingen, Ulm, Regensburg, and Munich, among other places. The Freiburg laboratory, regrettably, was discontinued, although it was one of the few that enabled young German students to collaborate with established vision researchers from other countries. Wolfgang Kurtenbach and Frank Stürzel had as many as six papers each, jointly published with senior faculty from the US, Canada, and Scandinavia before receiving their doctorate.

Finally, I will always be grateful to my collaborators for their loyalty and help. None of the research that came out of our laboratory could have been done without them. Numerous publications owe their existence to the long-standing scientific exchange with the laboratories in Boulder, Sacramento, Oslo, Trondheim, Dortmund, Sassari, Padua, and New York. The social side of science always meant a great deal to me. Looking over the past 35 years, I will not forget the unailing help received from my friends in the vision communities in Boston, Cambridge, MA, and Berkeley. I thank the University of Freiburg, the German Research Council, the Alexander von Humboldt-Foundation, the German Academic Exchange Program, and the other funding agencies for their most generous support. And I thank my family.

Summary

I have attempted to show how the study of simple perceptual phenomena enables us to learn more
about the neuronal processing of visual stimuli in the human brain. Examples include the Hermann grid illusion, illusory contours, figure-ground segregation, coherent motion, fading and filling-in, and large-scale color assimilation.

The term perceptive field is heuristically valuable as it provides the bridge from the phenomenon to the underlying receptive field organization. The correlation between the two is not just qualitative; it also enables quantitative comparisons. Gestalt phenomena that were observed 80 years ago have not lost any of their meaning; to the contrary, they even have gained in importance. With today’s knowledge of neuronal mechanisms, they serve as non-invasive tools to gain insight into the processes of how the visual system organizes the seemingly bewildering wealth of information from the outside world.

In his seminal article on visual perception and neurophysiology, Richard Jung (1973) published a table of neurophysiological correlates summarizing much of the Freiburg work. Given the speed of today’s progress and the enthusiasm of researchers in the field of vision (Chalupa and Werner, 2004), we have good reasons to hope that in the next 30 years the neuronal mechanisms and processes underlying visual perception will be largely unveiled.

Acknowledgements

I thank S.C. Benzt for transcribing my talk at ECVP 2005 in A Coruna (Spain). The additional help by W.H. Ehrenstein, E. Peterhans, B. Heider, J.S. Werner, A. Kurtenbach, C. Stromeyer, and B. Breitmeyer is greatly appreciated. Tobias Otte kindly modified and assembled the figures.

References


