Perception, 1999, volume 28, pages 1461 – 1492

DOI:10.1068/p2763

From elements to perception: Local and global processing in visual neurons†

Lothar Spillmann
Institute of Biophysics and Radiation Biology, Brain Research Unit, University of Freiburg, Hansastrasse 9, 79104 Freiburg, Germany; e-mail: spillman@uni-freiburg.de
Received 24 February 1998, in revised form 4 January 1999

Abstract. Gestalt psychologists in the early part of the century challenged psychophysical notions that perceptual phenomena can be understood from a punctate (atomistic) analysis of the elements present in the stimulus. Their ideas slowed later attempts to explain vision in terms of single-cell recordings from individual neurons. A rapprochement between Gestalt phenomenology and neurophysiology seemed unlikely when the first ECVP was held in Marburg, Germany, in 1978. Since that time, response properties of neurons have been discovered that invite an interpretation of visual phenomena (including illusions) in terms of neuronal processing by long-range interactions, as first proposed by Mach and Hering in the last century.

This article traces a personal journey into the early days of neurophysiological vision research to illustrate the progress that has taken place from the first attempts to correlate single-cell responses with visual perceptions. Whereas initially the receptive-field properties of individual classes of cells—eg contrast, wavelength, orientation, motion, disparity, and spatial-frequency detectors—were used to account for relatively simple visual phenomena, nowadays complex perceptions are interpreted in terms of long-range interactions, involving many neurons. This change in paradigm from local to global processing was made possible by recent findings, in the cortex, on horizontal interactions and backward propagation (feedback loops) in addition to classical feedforward processing. These mechanisms are exemplified by studies of the tilt effect and tilt aftereffect, direction-specific motion adaptation, illusory contours, filling-in and fading, figure–ground segregation by orientation and motion contrast, and pop-out in dynamic visual-noise patterns. Major questions for future research and a discussion of their epistemological implications conclude the article.

1 Introduction

Jung, Baumgartner, Creutzfeldt, Grüsser—the founding fathers of the Freiburg school of neurophysiology—they are all gone now within a span of only eight years (1986–1993). It is an appropriate moment to pause and look back. Based on my memories, I would like to present this personal account of the development of visual neurophysiology and perception during the last forty years, with an emphasis on research conducted in Germany. I am, of course, well aware that ground-breaking work in the same field was performed in several European countries, as well as on the other side of the Atlantic, in the United States. While these developments have been the subject of much discussion, many of the early experiments in single-cell visual neurophysiology were published in German journals and are therefore less known. This article claims to be neither systematic nor comprehensive. It totally ignores, for example, what has been done for many decades in EEG recording, and only briefly mentions the new imaging methods used to study functional brain topography in human observers. Rather, it attempts to balance the scale and promote a trend in vision research that has been dear to my heart: linking visual psychophysics and neurophysiology.

I will use selected examples to show how during the period under consideration the field of vision research has progressed from the study of elements to the study of perceptions. By elements I mean dots, lines, and edges; by perceptions—illusory contours,

† Based on an invited lecture at the 20th European Conference on Visual Perception, Helsinki-Espoo, Finland, 27 August 1997.

surfaces, and figures on a ground. This move from one to the other involves a change of paradigm: Instead of studying simple physical stimuli, vision researchers today increasingly use stimuli that elicit complex percepts (including natural scenes) to better understand how we perceive the world.

Progress in the visual sciences has been so fast that few may realise how little we knew just a generation ago. The celebrated concepts of parallel processing—the parvo and magno systems (colour/motion), the 'what' and 'where' systems (recognition/localisation), the over thirty visual areas in the brain—they all developed during the lifetime of ECVP. When I started university in 1958, the concept of the *receptive field* (first defined by Sherrington in reflex physiology) was largely foreign to experimental psychologists. This may sound surprising, as the major properties of visual receptive fields—such as spatial summation, lateral inhibition, and centre–surround antagonism—were already known from studies of ON- and OFF-units in the frog and cat retinae (Barlow 1953; Kuffler 1953). Why then did we not know more about visual processing at that time?

The problem was that few psychologists in Germany (and not just there) read the physiological literature, and, if they did, they could not easily relate it to visual perception. For example, to Metzger (1961) the transformation of the visual stimulus from a retinal mosaic of photoreceptors (comparable to a pointillistic painting) to a coherent surface in perception represented an *Aporie*—a problem that in principle cannot be resolved. Another example is Wohlfarth's (1932) important but little-known study of *Aktualgenese* or microgenesis (the perceptual emergence of small, brief, low-contrast stimuli presented in the peripheral field of vision), showing that percepts organise themselves from an undifferentiated *Vorgestalt* (pre-Gestalt) in the simplest, most regular, and balanced manner according to the principle of *Prägnanz*. How could one account for these earliest stages of figure–ground formation in terms of receptive-field properties? Even forty years later, we are just beginning to understand how Gestalt factors such as good continuation, closure, proximity, symmetry, and common fate may be physiologically implemented.

Wolfgang Köhler, the famous Gestalt psychologist, may have come the closest to a physiological approach to vision when he set out to record direct-current potentials from the skull of a human observer hoping to find an isomorphic correlate of perception (Köhler and Held 1949). Cortical visual maps had been known for a long time from the perimetric study of war victims with penetrating injuries of the occipital cortex (Poppelreuter 1917; Holmes 1918; von Szily 1918; Teuber et al 1960). However, it took many more years before physiologists could begin to give a detailed answer to the question of how the retinal image is transformed when it is 'projected' onto the surface of the brain (Fischer 1973; Tootell et al 1982; Fox et al 1987; Schwartz 1984, 1994). Despite his keen sense of perception, Köhler did not find it easy to accept the idea that myriads of individual neurons interconnected by a network of nerve fibres should carry the visual information in an orderly manner from the eye to the brain. When Hans-Lukas Teuber (1967) told him about the then new findings of Hubel and Wiesel, Köhler was skeptical. The assumption that highly selective neurons in the visual system should analyse ('dissect') a stimulus and mediate its contrast, polarity, brightness, colour, orientation, direction of motion, and depth, seemed to be too atomistic to fit into the framework of Gestalt psychology.

On looking back forty-five years later, it seems that we could have predicted much of what we know now. In fact, if one had to build a device capable of doing what our perception does for us—providing us with information on any of the stimulus attributes just mentioned and at the same time enabling us to make guided saccades to objects of interest—the use of highly selective detectors would be an attractive and plausible way to do it. However, the visual system is more complex than that.

1.1 *The pioneers*

In comparison to psychologists, physiologists had a much easier task unravelling the secrets of vision and putting it, step by step, on a firm basis. They had been exposed to the neuron doctrine of Ramon y Cajal (1893) for more than fifty years. Three papers prepared the ground for scientific study. Adrian and Matthews (1927, 1928) determined a visual receptive field for the first time by recording responses to two or more small light spots from the optic nerve of the conger eel as a function of stimulus separation. They found that the response latency for a given quantity of light remained the same regardless of whether it was concentrated into a crowded patch or spread out over several small areas, and that it was shorter than for each of the stimuli presented individually (spatial summation). Two years later, Hartline (1938, 1940) published two papers on the receptive fields of optic nerve fibres in the frog. Therefore, the question whether a receptive-field organisation also existed in the mammalian brain seemed not only timely but perfectly legitimate to physiologists. The first to lower an electrode into the visual cortex of the cat and record action potentials from a single neuron were Rudolf von Baumgarten and Günter Baumgartner in Richard Jung's laboratory in Freiburg.

Figure 1 is taken from the classic article by Jung et al (1952). The upper trace shows an original recording from a neuron in area 17. The thin horizontal line below marks the light stimulus. It can be seen that 20 ms after switching the light on, the neuron responded with an initial burst, followed by a few scattered spikes as the stimulus continued. The second trace refers to the local EEG, recorded with a longer time constant. Jung termed this kind of light-activated neuron, B-neuron (B for brighter). Its counterpart was called D-neuron (D for darker).

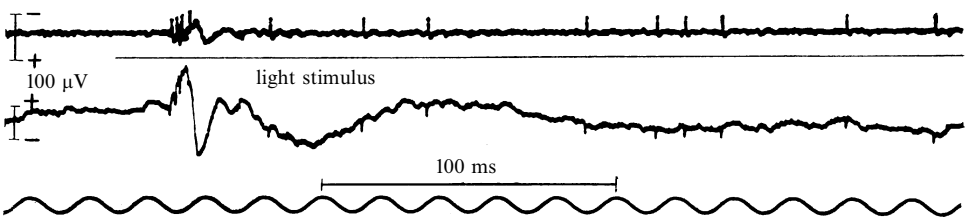


Figure 1. Action potentials of a cortical neuron in the cat in response to a continuous light stimulus (thin long horizontal line). Upper trace recorded with a short time constant, middle trace with a long time constant. Bottom line 50 Hz-time mark. (From Jung et al 1952.)

After this pioneering work it took seven more years until the next large step was taken by two research groups at the Massachusetts Institute of Technology (MIT) and the Harvard Medical School. The authors of the first paper were Jerome Lettvin, Humberto Maturana, Warren McCulloch, and Walter Pitts, and the title of their 1959 paper was "What the frog's eye tells the frog's brain". In this paper, the authors laid the groundwork for the question of how the anatomy and physiology of the frog retina and optic tectum might be related to the frog's vision (for a review see Grüsser and Grüsser-Cornehls 1976). This is when the name 'bug detector' came up among psychologists. The term is derived from Barlow's (1953) paper where he writes (page 86): "The receptive field of an 'on–off' unit would be nicely filled by the image of a fly at 2 in. distance and it is difficult to avoid the conclusion that the 'on–off' units are matched to this stimulus and act as 'fly detectors' ".

The second paper was by David Hubel and Torsten Wiesel (1959) on "Receptive fields of single neurones in the cat's striate cortex". This was the first in a long and systematic series of pioneering studies that eventually would earn their authors the Nobel prize in physiology and medicine. In the same year, Walter Rosenblith held a meeting at MIT on *Sensory Communication* (proceedings published in 1961) to which he invited a great

number of eminent physiologists, psychologists, physicists, and electrical engineers. Only one year later, in 1960, Jung and Kornhuber organised a conference on the *Neurophysiology and Psychophysics of the Visual System* (proceedings published in 1961) in Freiburg. Thereafter, the world of vision research was never the same.

The Freiburg conference brought together many distinguished scientists who later became leaders in the field. Among the neurophysiologists were Horace Barlow and Daniel Whitteridge from England; Russel De Valois, Robert Doty, and Edward MacNichol from the United States; and Gunnar Svaetichin from Venezuela. In addition to the organisers, the German researchers included Günter Baumgartner, Otto Creutzfeldt, Otto-Joachim Grüsser, and Ursula Grüsser-Cornehls (all from Freiburg); furthermore, there were Eberhardt Dodt from Bad Nauheim and Wolfgang Jaeger from Heidelberg. A good number of psychologists were also in attendance: Leo Hurvich, Dorothea Jameson, Wolfgang Metzger, and Hans-Lukas Teuber. And there was Kai Otto Donner from Finland, the noted electrophysiologist and father of Kristian Donner, organiser of the 20th EVCP in Helsinki.

1.2 *Feature encoding by receptive fields*

It was at the 1959 – 1960 conferences that the term *receptive field* evolved into a key concept for the understanding of vision and visual perception. It was also at these conferences that the foundations were laid for a functional correlation between neuronal firing patterns and visual perception in the tradition of Ernst Mach (1865) and Ewald Hering (1878). In retrospect, it can be said that the MIT and Freiburg conferences were milestones marking the beginning of modern visual neuroscience. The prerequisite conditions for Fechner's 'inner psychophysics' anticipated in his *Elemente der Psychophysik* (1860) had finally arrived, enabling researchers to tie the conscious percept not only to the physical stimulus (ie outer psychophysics), but also to the neurophysiological processes mediating it.

In the sixties and early seventies, vision scientists began to realise that visual neurons were specialised *feature detectors* (Barlow 1953) encoding dot, line, bar, and edge stimuli depending on their polarity, wavelength, orientation, movement direction, and lateral disparity. Devotees of visual Fourier theory might add spatial frequency, contrast, and phase (Braddick et al 1978; De Valois and De Valois 1990).[(1)]

As we now know, the term 'detector' was an oversimplification, as a single-neuron's response is always a function of several stimulus variables and therefore ambiguous. However, at the time, searching for candidate cells as the neural substrate of select visual phenomena became a major research strategy of many psychologists.

What were the sources prompting these rapid developments in the physiology and psychology of vision research? One source obviously was of a technical nature. The introduction of the microelectrode together with improved amplifiers and oscilloscopes enabled researchers to record from single neurons during controlled light stimulation of the eyes. Although the total number of cells from which recordings were made was relatively small, the basic conclusions drawn from these early studies still hold. This suggests that the responses obtained from a limited sample of neurons may be representative of the behaviour of a much larger population. In this context it is important to remember that most of these recordings were averaged over a large number of stimulus presentations, not unlike the signal averaging performed by the nervous system when it 'interprets' the responses of individual neurons.

[(1)] The Fourier approach is partly opposite to the feature detection approach: the former rests on the idea of general principles for image analysis common to biological and technical systems, whereas the latter builds on the idea of detectors evolved to extract specific features of 'biological interest'. Of course, this distinction is far from absolute. The 'feature detectors' elucidated by Hubel and Wiesel really represent the first steps in an alternative strategy for general image analysis, and the two schools converge in the idea of different neural 'channels'.

In recent years, the development of multiple-electrode techniques (Eckhorn et al 1988; Krüger 1990) and powerful computers, as well as their availability and ease of use, has enlarged the number of cells that can be studied simultaneously. Of course, just because one records from a dozen or so neurons at once, this does not by itself mean that one understands the nerve network (Krüger and Becker 1991). Also, without knowing what the nature of the sampling process is and how representative those numbers are, the real advantage of using multiple electrodes is difficult to assess. The key to modeling neuronal response patterns is the development of analytical tools for examining interactions and temporal synchronies among those neurons—not just the mere collection of data.

2 Neuronal correlates of visual perception

In addition to the technical advances, the other source which contributed greatly to today's understanding of visual function was conceptual. It implied that *single-cell responses are neuronal correlates of visual phenomena* and, vice versa, *visual phenomena are perceptual correlates of neuronal mechanisms*. This concept was most strongly advocated by Richard Jung, a clinical neurologist and neurophysiologist, and his two friends, Donald MacKay, a communications engineer from Keele, England, and Hans-Lukas Teuber, the MIT neuropsychologist (figure 2).

Figure 2. Left: Richard Jung (1911 – 1986). Right: Donald MacKay (1922 – 1987) in the middle, Hans-Lukas Teuber (1916 – 1976) on the right, and Sir John Eccles (1903 – 1997) in the background during the conference on "Brain Mechanisms and Conscious Experience" at the Vatican Scientific Academy in 1966. (From Creutzfeldt 1990.)

Together they would later edit the *Handbook of Sensory Physiology* (1971 – 1981) which remains a landmark achievement to this day. One continues to marvel how so many of the phenomena that had been demonstrated and described by sensory physiologists in the last century had been accounted for within a span of only twenty years after the first single-unit recordings.

The Freiburg school of neurophysiology contributed greatly to these early successes. By investigating the microphysiology of cortical neurons and their significance for vision and visual perception (Jung 1959), these researchers aimed to demonstrate that

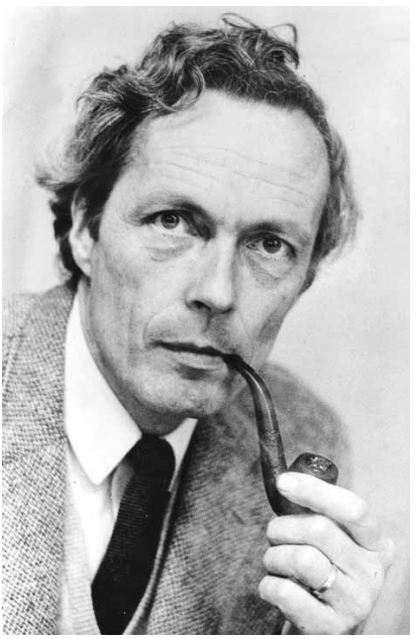
the neuronal response (ie firing rate) presumably underlying a given perceptual quality (eg brightness) varied in parallel with a given stimulus parameter (luminance). In quick succession, the visual systems of fish, rabbit, and cat were studied, not only to elucidate the processes underlying vision at the cellular level, but more specifically to find neuronal correlates of human perception.

What an exciting time it was for a young student to watch the neurologists at the end of a clinical day go to the crammed basement of the hospital and begin their neurophysiological experiments which often lasted until the early morning (Dichgans 1998). Encephale isolé preparations were the rule then (not to my pleasure), glass micropipettes were being used for recording, spike trains were recorded on film (not common then) and counted by hand to arrive at quantitative relationships. None of this research could have been done without the close cooperation of the ingenious Jan Friedrich Tönnies (formerly at the Rockefeller Institute of Medical Research and inventor of the differential amplifier) who developed many of the instruments; and the technical assistance, as well as active participation, of the ever-present engineer Hermann Kapp who had his workshop next door. Neurons could be heard crackling from late at night until the early morning hours. It was the time of fast discoveries, something new emerging almost every month. I remember illustrious visitors and guests: Denise Albe-Fessard, Ragnar Granit, Giuseppe Moruzzi, Henri Hécain, John Szentágothai, John Eccles, Donald MacKay, David Hubel. Many more signed the omnipresent guest book.

Grüsser was the first to recognise and defend—on philosophical grounds—the potential of a combined psychophysical and neurophysiological approach (Grüsser 1956; Grüsser and Grüsser-Cornehls 1973; for a review see Przybyszewski 1997). In his dissertation (1956) he clearly stated that although there can be no proof of a causal connection between objective neuronal responses and subjective observations, we may assume a mutual correlation ('wechselseitige Entsprechung') between one and the other, in the sense of Wundt's psychophysical parallelism. He quotes Wundt (1911, page 746): "Wherever systematic relationships exist between psychical and physical phenomena, they are neither identical nor can they be transformed into each other, as they are not comparable; however, they are referred to each other ('einander zugeordnet') in such a way that certain psychical processes lawfully correspond to certain physical processes, or as one may express it in a picture, both *go parallel with each other*" (translation and italics by the author).

In 1961, Grüsser and Carmen Rabelo, a doctoral student from Venezuela, showed that the brightness enhancement of a light flickering at medium temporal frequencies (Brücke–Bartley effect) correlated with the peak discharge rates of retinal and cortex neurons in the cat (Grüsser and Creutzfeldt 1957). Figure 3 portrays Otto Creutzfeldt and Otto-Joachim Grüsser, after they had left Freiburg and became directors of their respective institutes in Göttingen and Berlin.

Further research on the possible neuronal correlates of perceptual phenomena developed quickly in the late fifties and sixties. For example, the logarithmic increase of the spike rate in retinal and geniculate neurons with physical light intensity (Fechner's law); the periodical change of B- and D-discharges corresponding to the Charpentier, Purkinje, and Hess afterimages following a bright flash (Grüsser and Grützner 1958); and the enhancement of neuronal activity near an edge, ie border contrast (Baumgartner 1961), were demonstrated at that time. Sinusoidal flicker and moving gratings—the preferred stimuli of the next three decades—were introduced in Freiburg as early as the late fifties. There might have been more. In a memorable retrospective, Jung (1975) muses why the orientation specificity of the cortical neurons that could have been easily found by a single qualitative experiment was missed by the Freiburg researchers in 1958.



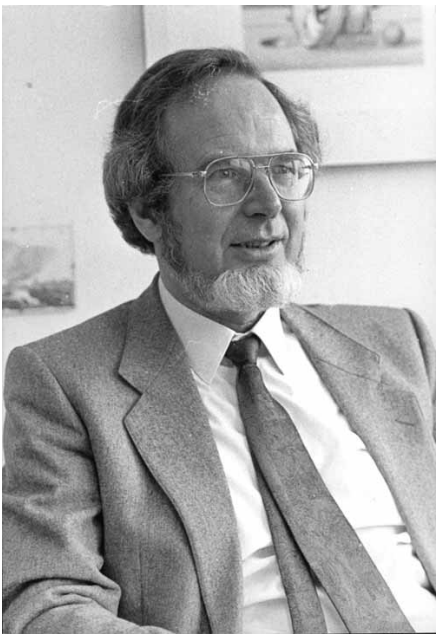


Figure 3. Left: Otto Creutzfeldt (1927 – 1992). (Courtesy of Max Planck Institute for Biophysical Chemistry, Göttingen.) Right: Otto-Joachim Grüsser (1932 – 1995). (Courtesy of Professor U Grüsser-Cornehls.)

Jung's (1973) large handbook article summarises the correlations between visual phenomena and their presumed neuronal mechanisms for the first fifteen years (see his figure 1, tables 1 and 2). A good example is his early distinction between two neuronal subsystems for the perception of 'brighter' and 'darker' (Jung 1961a, 1961b). However, it took many more years for this distinction to become generally accepted.

Converging evidence for separate B- and D-systems came from three different disciplines: In psychophysical experiments, Magnussen and Glad (1975a) demonstrated brightness and darkness enhancement (ie the Broca-Sulzer effect) for increment and decrement stimuli, and Ehrenstein and Spillmann (1983) similarly obtained different time thresholds for the two polarities. At about the same time, Nelson et al (1978) and Wässle et al (1981) found by histological techniques that ON- and OFF-ganglion cells make their synaptic contacts in different sublayers of the cat retina. Finally, Schiller (1982) showed that the ON-system could be selectively inactivated by injecting a glutamate agonist, 2-amino-4-phosphono-butyrate or APB, into the eye, thereby blocking the signal transmission between photoreceptors and ON-bipolar cells. He and his collaborators (1986) went on to correlate this blocking effect with the animal's behaviour: monkeys treated in this manner made saccades only to luminance decrements, not increments, suggesting that they could see only stimuli that were darker, but not brighter than the background. These results provided strong evidence that the ON- and OFF-channels form visual subsystems that are structurally and functionally independent all the way from the retina to the striate cortex. It appears that these parallel channels have evolved to provide faster information and a greater dynamic range from the photoreceptors to the central nervous system by using excitatory processes for both increases and decreases in luminance.

2.1 *Hermann grid illusion*

In a bold attempt to link the newly found receptive-field organisation in cat to human visual perception, Baumgartner, in 1960, took on an illusory brightness phenomenon that had resisted explanation for ninety years. He proposed that the dark spots in the well-known Hermann grid illusion (Hermann 1870) could be explained by the increased lateral inhibition at the intersection, relative to a bar, resulting in less brightness. This increase is schematically illustrated in figure 4 (left). Assuming that the illusion was strongest when the width of the intersecting bars equalled the diameter of the receptive-field centre, Baumgartner employed the Hermann grid illusion for investigating—what he surmised—was the receptive-field organisation in human vision.

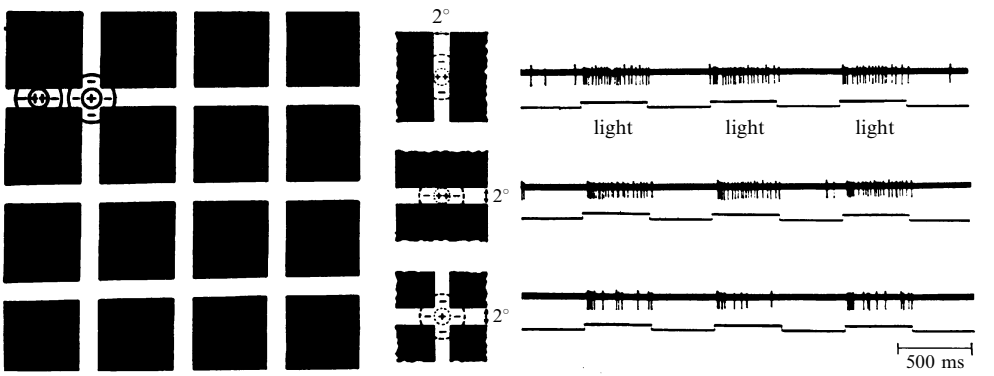


Figure 4. Left: Hermann grid showing dark illusory spots at the intersections. The receptive field of an on-centre neuron receives more lateral inhibition (−) when illuminated by an intersection than when illuminated by a bar, hence the darkening. Right: A cortical neuron of the cat with a concentric receptive field responds equally well to a vertical and a horizontal bar, but responds much less when both bars are presented simultaneously. (From Baumgartner 1990.)

The procedure was simple. Subjects walked towards a Hermann grid and away from it and, in this manner, determined the distance at which the illusion reached its maximum. From this distance, Baumgartner calculated the average diameter of foveal receptive-field centres. Diameters turned out to be quite small, about 5 min of arc (see also Spillmann 1971). This small size explains why the dark spots tend to disappear in foveal vision: the reason is that most grids are too wide to differentially stimulate the receptive fields illuminated by the bar and the intersection—hence no illusion. Towards the peripheral retina field centres increase in size, up to 3 deg (Jung and Spillmann 1970). This change of size agrees with the relative increase of neurophysiologically determined field centres of single cells in cat and monkey (Spillmann et al 1987).

To confirm his hypothesis Baumgartner recorded from a single cell in area 17 of the cat. The upper trace in figure 4 (right) shows the response to a vertical bar, the trace in the middle the response to a horizontal bar. Both responses are equally strong. However, when the two bars were presented together, the neuronal response was significantly reduced (bottom). This reduction in firing rate is consistent with the perceived darkening at the intersection. There are, of course, discrepancies between this simple explanation, on the one hand, and actual results, on the other. For example, it has been demonstrated that the strength of the Hermann grid illusion grows with an increasing number of aligned intersections, calling for an additional, global contribution (Wolfe 1984; for a review see Spillmann 1994).

Baumgartner's use of the Hermann grid illusion as a psychophysical tool for probing the neural circuitry of the human visual system has now entered the textbooks (eg Fiorentini et al 1990; Sekuler and Blake 1994), next to the light and dark Mach bands—a classic example of a correlation between percept and neural processing

(Ratliff 1965). The study of these contrast phenomena opened the door for using other illusions as well. An example is Wertheimer's phi phenomenon. By measuring the largest distance between two alternating stimuli across which apparent motion could be perceived, I attempted in my dissertation to determine the size of receptive fields of human movement-sensitive neurons. It turned out to be about 20 times larger than the receptive-field size obtained with the Hermann grid illusion (Kornhuber and Spillmann 1964).

To distinguish a neuronal receptive field—as defined by the response of a single cell to a moving or flashing light spot—from its correlate in human perception, Jung and Spillmann (1970) introduced the term *perceptive field*. In analogy to the receptive field, the perceptive field refers to an area on the retina (and in visual space) within which a change of stimulation changes the resultant percept (or threshold) in monkey and human observers. Its size and response properties can be inferred from psychophysics, such as the Westheimer function (Westheimer 1965; Ransom-Hogg and Spillmann 1980). Like the receptive field (Kuffler 1953; Rodieck 1965), the perceptive field is thought to possess an antagonistic centre–surround organisation. However, unlike the neurophysiologically defined receptive field, it reflects the simultaneous activity of a large number of neurons contributing to a given percept (Spillmann et al 1987). Depending on the stimulus, these neurons may reside at different levels within the visual system (retina, LGN, visual cortex). The assumption that many neurons interact synergistically (ie like one) to produce a given percept is analogous to Barlow's (1972) concept of the most sensitive neuron.

When I presented these ideas to David Hubel and Torsten Wiesel in 1964, there was a mixed response. While the latter took a cautious interest, the former was skeptical [about 25 years later, Livingstone and Hubel (1987, 1988) would publish their pivotal papers on the functional correlates of the parvocellular and magnocellular streams]. His advice then was: Never mind percepts, do straightforward physiology. This was surprising because the *Hubel and Wiesel detectors* as they came to be known, appeared to lend themselves so readily to an explanation of a number of well-known perceptual effects and aftereffects that could be used to noninvasively probe the human visual system. Let me give two examples.

2.2 *Tilt effect and tilt aftereffect*

The first example is the tilt aftereffect. Gibson and Radner (1937) found that, after adapting to a slightly tilted line, a truly vertical line presented thereafter appeared to be tilted in the opposite direction. Magnussen and Kurtenbach (1980a) in the Freiburg laboratories

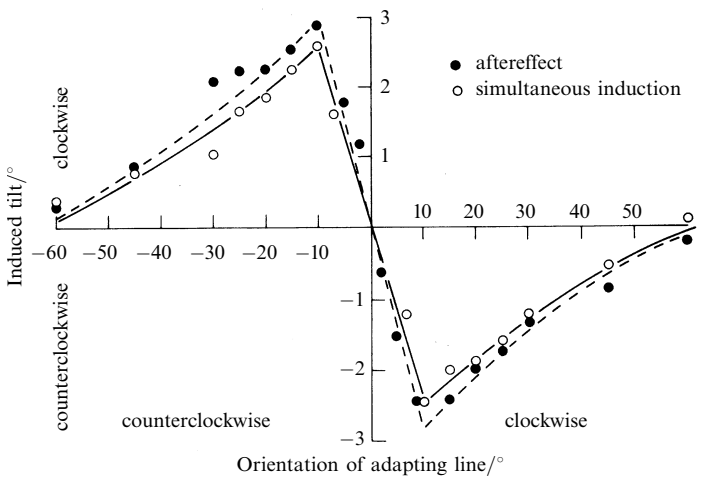


Figure 5. Tilt aftereffect and tilt effect after Gibson. Induced tilt of a test line plotted as a function of the orientation of an adapting line presented before (filled circles) or simultaneously with the test line (open circles). (From Magnussen and Kurtenbach 1980a.)

quantified this effect. In figure 5 (filled circles), the amount of induced tilt of the test line is plotted as a function of the orientation of the adapting line. For example, when the adapting line was tilted 10° clockwise, the test line appeared to be tilted almost 3° counterclockwise. For other adapting orientations, the induced tilt was smaller. Note that the curve returns to the baseline at 60°.

In that same study, Magnussen and Kurtenbach obtained nearly identical results when the adapting line and the test line were presented simultaneously (open circles). This tilt effect had first been reported by Hofmann and Bielschowsky (1909), who found that a line representing the subjective vertical was set to the opposite side when viewed against a background of oblique contours. The same effect was later exploited by Witkin (1959) in his well-known rod-and-frame experiment.

In figure 5, the two curves for tilt and tilt aftereffect superimpose almost perfectly. The close agreement, with and without preceding adaptation, speaks against an explanation of the tilt aftereffect by neuronal 'fatigue' or 'satiation' (the neuron becomes less sensitive because of its own previous activity). Instead, it suggests that both effects are based on inhibitory interactions between orientationally tuned units in the human visual system (Blakemore et al 1970; Blakemore and Tobin 1972). Magnussen and Kurtenbach (1980b) provided an even more compelling argument in support of the inhibition hypothesis by showing that a second adapting line could weaken the effect exerted by the first, presumably by disinhibition. In their experiment they adapted subjects to two stimuli simultaneously, holding the orientation of one constant, while varying the orientation of the other. The fatigue hypothesis would predict an increase in the tilt aftereffect with dual-orientation adaptation as compared to adapting to the most effective of the two orientations alone, whereas the inhibition hypothesis predicted a decrease in aftereffect magnitude. The results showed a reduction in the aftereffect magnitude in accordance with the latter.

2.3 *Perceived direction of motion*

Levinson and Sekuler (1976) demonstrated an effect analogous to the tilt effect, in the domain of motion perception. They adapted to a large field of moving dots drifting in one direction and subsequently tested the effect of adaptation with the same field of dots moving in any of several other directions. In figure 6, the perceived shift in the direction of the test field is plotted against the direction of the adapting field. No change in perceived direction occurred when test and adaptation directions were the same (zero on abscissa). However, apparent shifts of varying size were observed for test directions in the vicinity of the adaptation direction. For example, when the angle

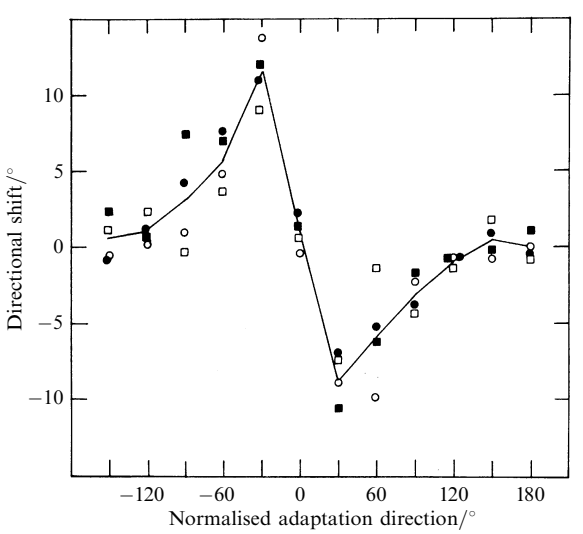
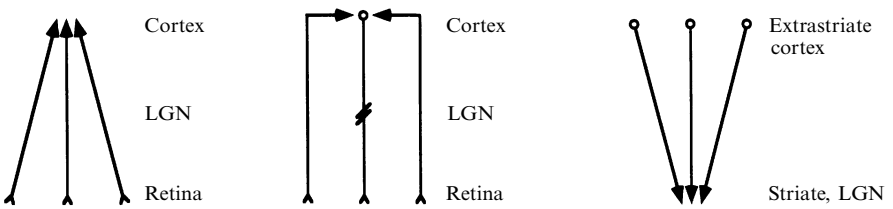


Figure 6. Directional shift of a test field of moving dots plotted as a function of the direction of an adapting field of moving dots. Zero on the abscissa marks the point when test and adapting directions were the same. Positive values, anticlockwise; negative values, clockwise direction. (From Levinson and Sekuler 1976.)

between the two kinds of stimuli was 30°, the test field appeared to be shifted 10° away from the direction of adaptation, resulting in a 40° apparent difference. This perceptual displacement is three times larger than for tilt. Note that the positions of the maximum and minimum as well as the points where the curve asymptotes are also three times further away from zero. These differences suggest a much broader tuning range of the motion channel than of the orientation channel.

What might be the neuronal mechanisms underlying these effects? Current research has focused on three kinds of hypothetical mechanisms as depicted in figure 7 (for a review see Spillmann and Werner 1996). These are: converging feedforward projection (Hubel and Wiesel 1965; reviewed in Hubel 1988), recruitment of horizontal connections (Ts'o et al 1986), and backward propagation from higher to lower levels (Tononi et al 1992; Munk et al 1995) including the lateral geniculate nucleus (Murphy and Sillito 1996). The study of these mechanisms represents a shift in paradigm and has contributed greatly to a better understanding of large-scale perceptual phenomena during the last ten years. In the following section I describe several well-known examples of such phenomena as they might apply to one or several of these mechanisms.



(a) Converging feed-forward connections (b) Horizontal intrinsic connections (c) Reentrant (feedback) connections

Figure 7. Three hypothetical mechanisms for long-range interaction: (a) converging feedforward projections as the basis for new receptive-field properties emerging at higher levels; (b) cortico-cortical interaction by recruitment of lateral connections to explain filling-in of contours and surfaces; (c) backward propagation from higher to lower cortical levels to account for perceptual grouping (binding) and figure – ground segregation.

3 Long-range interactions: beyond the classic visual receptive field

The tilt aftereffect and the direction aftereffect are most plausibly interpreted as manifestations of feedforward interactions between neighbouring orientation and movement detectors. There is much evidence that orientation-specific responses in the cat visual cortex can be facilitated or inhibited by line or grating stimuli presented *outside the classical receptive field* (Blakemore and Tobin 1972; Fries et al 1977). More recently, Gilbert and Wiesel (1990) obtained substantial shifts of the preferred orientation away from the peak orientation when a second line of different orientation from the test line was shown in the outer surround. These results show that the preferred orientation of a given neuron is not fixed but dynamic, and depends on the context of presentation.

There had long been hints in the literature at contextual modifiability of a neuron's response (for a review see Allman et al 1985a). References to 'silent regions' (Barlow 1953), 'unresponsive areas' (Maffei and Fiorentini 1976), and responses from beyond the classic visual receptive field (Nelson and Frost 1978) had all suggested the existence of modulatory influences from a retinal area much larger than the concentric receptive field (see also Hammond and MacKay 1981). The best examples of such long-range interaction were perhaps the periphery (McIlwain 1964) and shift effects (Krüger and Fischer 1973; Barlow et al 1977), showing that the responses of a cat retinal ganglion cell to a central light spot could be facilitated by movement of a 'remote' stimulus many degrees away [for a possible analogue in human vision see Breitmeyer and Valberg (1979) and Valberg and Spillmann (1982)].

Regrettably, these early ideas did not receive as much attention as they deserved because neither the physiological nor the psychological *Zeitgeist* was ready to deal with them. A receptive field at that time was considered a fixed structural entity by most researchers, limited by the dendritic tree of the neuron, and it was difficult to conceive of additional inputs from outside the receptive field capable of modifying the response through contextual stimuli. This, however, was a prime requirement if neuronal response patterns were to account for large-scale perceptual phenomena. The breakthrough occurred with the neurophysiological study of illusory contours by Günter Baumgartner and his co-workers Esther Peterhans and Rüdiger von der Heydt, in 1984. Their discovery of neurons in area V2 of the macaque responding to what we perceive as partially occluded patterns bounded by illusory contours, was a major achievement that carried neurophysiology beyond the elementary dot, line, and edge stimuli used in previous decades.

3.1 *Illusory contours*

I vividly remember when in the summer of 1982 Gaetano Kanizsa (shown with Günter Baumgartner in figure 8) and Walter Gerbino from Trieste gave a seminar in the Neurological Clinic in Zurich on what later became to be known as Kanizsa figures. Walter H Ehrenstein, who was intimately familiar with illusory contours and brightness enhancement through his father's work (W Ehrenstein 1941) and I had driven over from Freiburg to listen to them. Gerbino gave the talk because Kanizsa felt that his English was not up to the task. However, in the discussion he repeatedly argued that there was no need for a physiological basis of illusory contours and brightness enhancement. At one point he held up a Kanizsa triangle in front of us asking in German: *Können Sie das mit Einzelzellen erklären?* (Can you explain this by single neurons?). A short time thereafter, a first answer to Kanizsa's challenge was given at the 5th European Conference on Visual Perception (Peterhans et al 1982). Two years later the full report by the Zurich group appeared in *Experimental Brain Research* (Baumgartner et al 1984) and in *Science* (von der Heydt et al 1984).

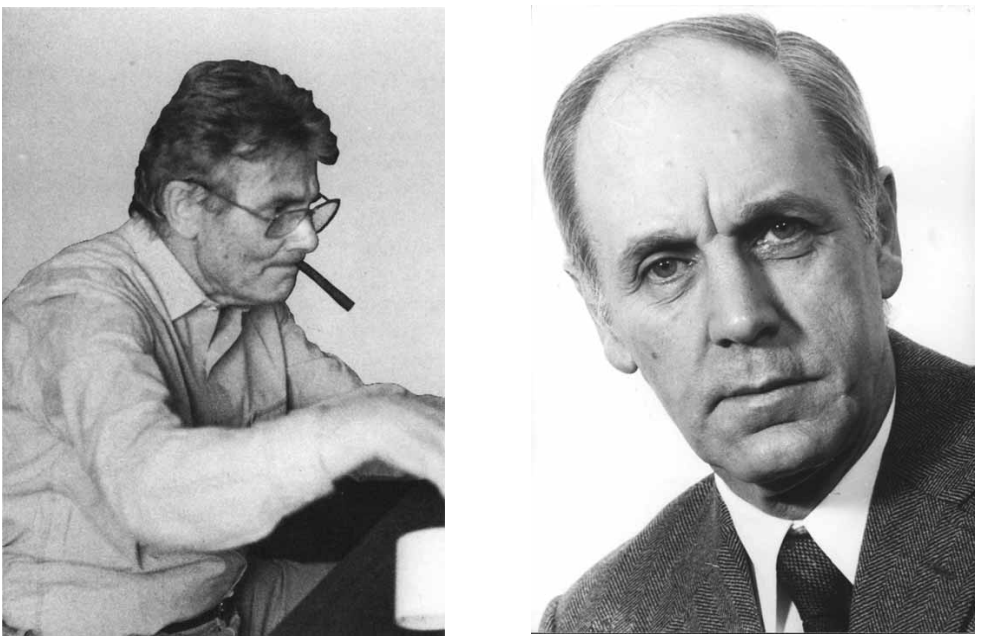


Figure 8. Left: Gaetano Kanizsa (1913 – 1993). (From Sumi and Noguchi 1996.) Right: Günter Baumgartner (1924 – 1991). (Courtesy of Neurological Clinic Zurich.)

Figure 9 shows the experimental stimulus (lower left). Under regular conditions, this stimulus elicits the perception of a bright bar delineated by illusory contours connecting the upper and lower notches across the gap. For a control, a physically continuous bar was used [as shown in (a)]. On the right is the response of a neuron in area V2 of the monkey. Each time when the continuous bar was moved across the receptive field there was a strong and reproducible discharge. When the same bar was used, but now with its middle section missing, the response pattern was similar, although less pronounced. This is surprising, because under these conditions there should have been no response at all as the neuron's receptive field (defined by a moving bar of optimal length, width, orientation, and contrast) was never actually stimulated. Apparently, the cell must have received orientational information from outside its receptive field. When the upper and lower halves of the stimulus were closed off by thin orthogonal lines [as shown in (c)], the neuronal response fell to its resting level. Likewise, no illusion could be perceived under these conditions (lower right). The Zurich group went on to explore also the abutting grating illusion, the Kanizsa triangle, and the Ehrenstein illusion in this way (Baumgartner 1990; for psychophysical data see Soriano et al 1996).

From their results Baumgartner et al (1984) concluded that, in addition to a local receptive field, there was a larger, global 'response' field that takes into account information from the outer surround. They proposed that neurons sensitive to line ends mediated the perception of illusory contours. The significance of this finding becomes immediately clear if one thinks of partially occluded objects as they frequently occur in nature. To extract a biologically useful representation of such an object in perception requires a neuronal mechanism capable of encoding physically unconnected parts as belonging to one and the same stimulus (Spillmann and Dresp 1995). This ability is likely to be cortical as we can segregate figure from ground even if the stimuli are presented interocularly (Kovács et al 1996). Without being able to extract wholes from parts, we could never hope to perceive objects perturbed by noise, break the camouflage—say—of a Dalmatian dog on a snowy surface, and manoeuvre around the world. These are then examples of how vision provides us with superior representations of the world not inspite of, but because of nonveridical image processing (Dresp 1997).

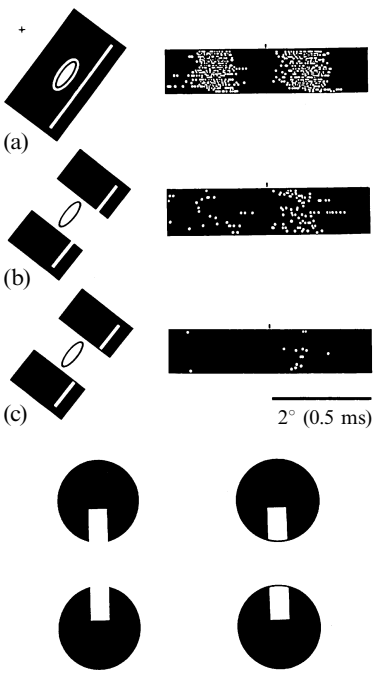


Figure 9. Top: Response of a neuron in area V2 of the monkey to a continuous bar (a), the same bar with its centre section missing (b), and the top and bottom sections of the incomplete bar, this time sealed off by thin orthogonal lines (c). Note the similarity in response for (a) and (b), although the response field in (b) (oval) is never directly stimulated. Bottom: Illusory contours appear to connect the upper and lower notches (left), but are abolished by thin closing lines (right). (From von der Heydt 1987.)

Up to then, perceptual filling-in of gaps was tentatively explained either by the Gestalt factors of good continuation and proximity (bottom – up), or by problem solving (top – down) strategies (Gregory 1987). It now seems that neural processes such as activation of end-stopped cells (Baumann et al 1997) may cooperate with mechanisms integrating information from similarly oriented receptive fields to enable these kinds of perception (Schmidt et al 1997). In support of these ideas, Dresp and Bonnet (1995) demonstrated psychophysically that a near-threshold line when superimposed onto an illusory contour will be more easily detected, in accordance with subthreshold summation. Furthermore, Dresp (1993) showed that a subthreshold target line presented collinearly with one or two inducers became visible presumably owing to lateral facilitation between oriented perceptive fields.

Using the Westheimer function, Yu and Essock (1996) and Yu and Levi (1997) have recently measured the spatial extent of such interactions in an attempt to define the perceptive fields of end-stopped cells in human observers (see also Soriano et al 1996). In analogy to Westheimer's original study (1965), log threshold for a target line first increased with background length, reached a peak, and then decreased again before levelling off. The background at which the curve peaked was taken as a psychophysical measure of the perceptive field centre while the background length at which the curve reached a plateau was interpreted as a measure of the centre plus end zones. For a target 10 min of arc long presented perifoveally, the length of the centre was found to be approximately 18 min of arc, while the total length was approximately 45 min of arc. Results suggest that units similar to those found in the monkey may also exist in the human visual cortex.

3.2 *Area (surface) contrast*

A time-honoured example requiring long-range horizontal interactions is *simultaneous contrast*, first described in the last century by Goethe (1810) and Hering (1878). Figure 10 shows four squares all of the same luminance, but appearing to be different in brightness because of the variable contrast to the background. A similar effect can be demonstrated for colour. How can these effects be explained neurophysiologically?

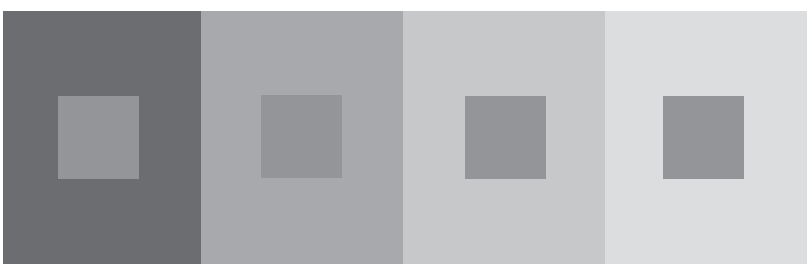


Figure 10. Hering's (1878) demonstration of simultaneous brightness contrast. The four inner squares have the same luminance, but appear to be of different brightness because of their contrast to the background. (From Schober and Rentschler 1972.)

This question was of great interest to Creutzfeldt's group in Göttingen, which over the years had demonstrated numerous relationships between perceptual phenomena on the one hand and the responses of parvo and magno cells on the other (eg Lee et al 1990). In the lateral geniculate nucleus of monkeys, the Göttingen group found that the neural response to a coloured stimulus could be modified by the presentation of a large steady surround outside the classical receptive field. Specifically, the response of LGN units changed in a way suggesting that the neuron signalled induced colour of the stimulus rather than its spectral properties (Valberg et al 1985; Creutzfeldt et al 1991; Kastner et al 1992). Thus, it appears that the response properties of these lower-level

neurons are consistent with perceptual phenomena such as colour contrast and colour constancy, features that had previously been attributed to extrastriate V4 neurons (Zeki 1983). A well-known example is Land's (1983) Mondrian pattern where a given patch is perceived as 'red' regardless of changes in illumination.

In addition to the study of patches of different colour as in a Mondrian one might ask how sustained perception of brightness and colour of large uniform areas is mediated. It is generally assumed that most neurons in areas V1 and V2 respond strongly to lines and edges, but respond poorly or not at all to constant illumination within their receptive fields. Why then do we see uniform surfaces and not mere outlines [ie Marr's (1982) primal sketch]? A plausible answer is: because of *filling-in* through long-range interactions from the edge (Spillmann and Werner 1996; Pessoa et al 1998). Indeed, when a steady stimulus of uniform luminance was shown within the classical receptive field while the background luminance was modulated well beyond the receptive-field area, the response of the neuron to the uniform stimulus could be modified (Paradiso et al 1996; Rossi et al 1996). This finding indicates long-range interactions between cortical neurons bridging the size of local receptive fields.

There is a large body of psychophysical studies in human observers showing that brightness and colour can be induced from the surround (eg Magnussen and Glad 1975b; De Valois et al 1986; Rossi and Paradiso 1996). The stimuli used in these experiments were centre–surround configurations or black-and-white gratings. By modulating the luminance of the surround, the brightness of the enclosed area(s) could be made to perceptually change in counterphase (Rossi and Paradiso 1996), not unlike an afterimage surrounded by a contrast-reversing annulus (Gerling and Spillmann 1987). Low spatial ($0.03-2$ cycles deg^{-1}) and temporal (< 2.5 Hz) frequencies were best. Induction time depended on distance, suggesting a speed of brightness propagation between $80-180$ deg s^{-1} (Paradiso and Nakayama 1991; Paradiso and Hahn 1996; Rossi and Paradiso 1996). On the other hand, Davey et al (1998), using the Craik–O'Brien–Cornsweet illusion to estimate the speed of brightness propagation, give a much lower value of only about 20 deg s^{-1}.

A highly simplistic mechanism that could potentially account for these observations is illustrated in figure 11. Shown (on the left) are three neurons in the visual cortex of the cat. Normally, each cell responds only to illumination of its receptive field and, thus, deafferentation of a cortical cell by laser photocoagulation of the retina would render this cell unresponsive (right). As a consequence of the laser burn, there would be a small, irreversible scotoma in visual perception. However, we now know that this loss of function can in part be compensated. For example, in the cat, it was found that after only a few minutes a massive reorganisation took place causing the deafferented cell to resume firing when light fell onto adjacent sections of the retina (Kaas et al 1990; Gilbert and Wiesel 1992).

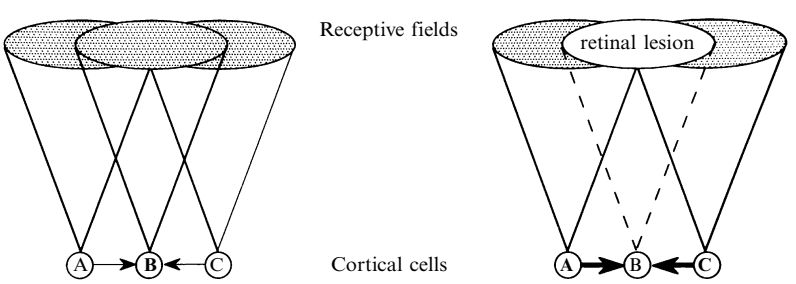


Figure 11. Model for filling-in of a scotoma by intracortical horizontal connections (schematic). Shortly after a retinal lesion, the deafferented cell (B) can be reactivated by illumination of the neighbouring areas through signals from A and C (thick arrows, right). As a consequence, the scotoma becomes invisible. Sustained brightness perception on uniform surfaces (left) may be similarly explained by maintained edge signals from the surround. (From Spillmann and Werner 1996.)

It thus appears as though cells that had their receptive fields in the lesioned area were now connected to portions of the retina corresponding to regions outside the scotoma (Eysel et al 1998).

One way to explain this *reactivation by remapping* is by assuming that signals travelling from neighbouring receptive fields to cells A and C are passed on in the cortex to cell B through long horizontal (tangential) connections. These cortico-cortical connections are assumed to be functionally present all the time; however, in the case of a local deafferentation, their influence may become potentiated owing to disinhibition. In this manner, the silenced cell B would acquire a receptive field that is displaced relative to and larger than its former receptive field. As a result of this functional reorganisation, the visual scotoma is thought to fill in from the surround so that a uniform surface would be perceived despite the absence of signals from the lesioned area (Safran and Landis 1996). Actually, many more cells and receptive fields would have to be considered to provide for this kind of neuroplasticity.[(2)]

3.3 *Filling-in and fading of artificial scotomata*

Horizontal axons (up to 7 mm long) providing lateral synaptic inputs have indeed been found in the cat and monkey cortex (Gilbert 1992; Lund et al 1993). Under normal stimulus conditions, the same mechanism that is thought to be responsible for the filling-in of a retinal scotoma may underlie the perception of uniform surfaces. Let us take again cell B (figure 11, left). As long as there is a signal propagating the information from the edge (cells A, C), the brightness and colour within the enclosed area (receptive field of B) would be kept alive. However, if the edge signal decreases owing to adaptation (no eye movements), the enclosed area would assume the brightness and colour of the surround and thereby become invisible (ie fading). Curiously, the model does not explain why only the enclosed figure, not the ground, is affected by this process. Only if there are no borders at all as in a *Ganzfeld*, brightness and colour across the entire visual field will rapidly fade and ultimately be replaced by one's *Eigengrau* (Knau and Spillmann 1996, 1997).

Fading and filling-in of enclosed areas are exactly what is perceived with strict fixation. Neumeyer and Spillmann (1977) and Ramachandran and Gregory (1991) showed that in the absence of eye movements even large uniform areas (so-called *artificial scotomata*) tend to fill in and within seconds become embedded in the background. For example, a centrally fixated, red disk presented on a green background will rapidly disappear from vision (especially if surrounded by a diffuse border) and be replaced by a uniformly green surface (Krauskopf 1963).

Ramachandran and Gregory (1991) demonstrated that fading was not restricted to a uniform background—on textured backgrounds it occurred as well. Even more surprising, a grey target presented on the background of dynamic visual noise, such as a detuned TV set, faded from view within seconds. This was unexpected as the target contour was redefined with each new frame and thus should have persisted over time. However, the opposite was the case: On the dynamic noise background fading occurred *faster* than on a uniform background (Spillmann and Kurtenbach 1992), possibly owing to adaptation of neurons processing kinetic contours (Allman et al 1985b; Marcar et al 1995). Even more intriguing, when observers so adapted viewed a plain surface, they perceived graininess ('dust') and dynamic twinkle in the area corresponding to the filled-in patch (eg Hardage and Tyler 1995). This aftereffect spread over an area as large as the entire hemifield, suggesting long-range horizontal interactions (Tyler and Hardage 1998).

[(2)] An alternative explanation of short-term plasticity in terms of an overall increase in cell responsiveness, rather than a dynamic alteration of receptive-field structure, has been proposed (DeAngelis et al 1995). As for long-term plasticity by sprouting see Eysel and Schweigart (1999).

What may be the neurophysiological mechanism underlying such extensive spreading? Fading and filling-in in monkey and man were studied by De Weerd et al (1995, 1998) who used the static stimulus shown in figure 12. The monkey had been trained to fixate a fixation point (FP) and to release a lever as soon as the white square disappeared from vision. Figure 13 shows the responses of a neuron in area V3. The continuous line represents the neuronal response obtained when the artificial scotoma in the stimulus was present, whereas the dotted curve shows the response when the artificial scotoma was absent (control). In both cases, the receptive field of the neuron was located completely inside the white square. Initially, the neuronal activity elicited by the stimulus plus artificial scotoma was low. However, within seconds the response increased and approached the firing level for the control stimulus, at the same time when human observers reported fading of the white square (shaded area). The authors therefore propose that the increase of the neural activity reflects perceptual filling-in (De Weerd et al 1995).

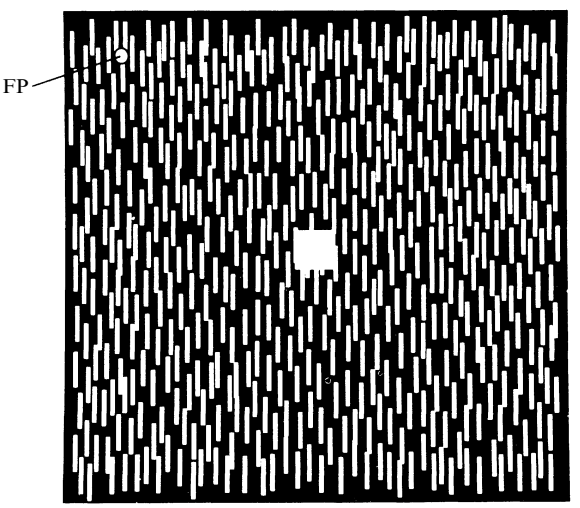


Figure 12. Fading and filling-in of an artificial scotoma on a textured background. The white square disappears from view after briefly fixating on FP. (From De Weerd et al 1995.)

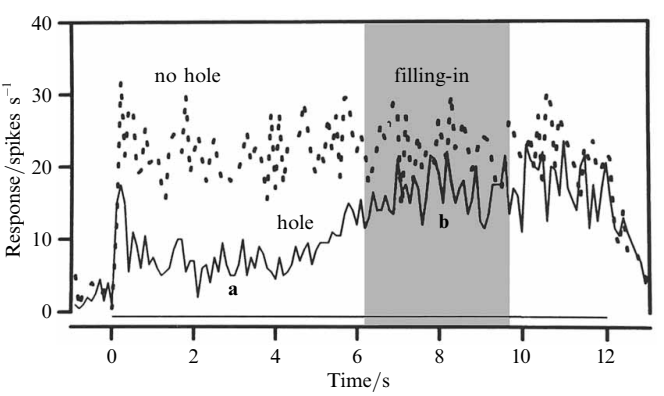


Figure 13. Response of a cell in area V3 of the monkey during fixation. The continuous curve refers to the stimulus shown in figure 12 (with the white square), the dotted curve to the same stimulus but without the square (texture only). The receptive field of the neuron was located well within the square. The shaded section marks the time when the square faded for human observers. (From De Weerd et al 1995.)

3.4 *Figure – ground segregation by orientation and motion contrast*

What about the opposite of fading: *pop-out and salience* of a stimulus? Van Essen et al (1991) and Lamme (1995) studied this question in the monkey using *orientation contrast*. Figure 14 (from Lamme) shows two kinds of stimuli, one that differs from the orientation

of the background by 90°, and another that is collinear with the background. (The thin frames delineating the stimuli were not presented.) The response of a representative cell in area V1 is shown on the right of the stimulus. As can be seen, the neuron responded more strongly when the stimulus area and the background were oriented orthogonally as compared to collinearly. Note that the orientation of the stimulus in figure 14 was the same in conditions (a) and (b) on the one hand and (c) and (d) on the other; only the orientation of the background had been changed. As in the previous experiment, the classic receptive field of the neuron (the small black rectangle) was always inside the stimulus area so that the border defined by the difference in orientation fell well outside that receptive field.

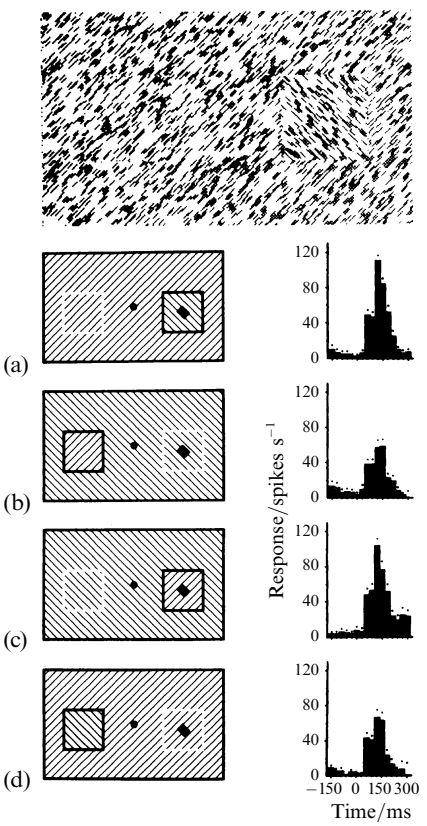


Figure 14. Response of a neuron in area V1 of the monkey to a textured stimulus. Boxes (a) through (d) show schematically the stimulus (illustrated by a thin frame that was, however, not presented) surrounded by a background of a different or the same orientation. The black oblique rectangle illustrates the receptive-field centre plotted by moving a black bar on a white background. Fixation was on the central black dot. The cell response to the stimuli (on the right of the box) is enhanced when the stimulus is defined by orientation contrast to its surround. (Modified—after Lamme 1995.)

In agreement with these findings, Sillito et al (1995) obtained 'supraoptimal' responses in V1 when the excitatory ('focal') receptive field of the cell was stimulated by lines of one orientation and the outer surround by lines oriented at right angles (ie junctions and corners). Different contributions of centre and surround reflecting the dynamics of the interaction dominated the early stages of the neuronal response. It appeared that the global presence of the stimulus was signaled first, followed by the response to the spatial discontinuities. A psychophysical correlate of crossed-orientation interaction has recently been demonstrated (Wolfson and Landy 1998).

Figure 15 additionally shows examples of *motion contrast* in the cat (Kastner et al 1997). The first column shows a strong response to a vertical bar placed in the receptive field of a neuron and moving in the preferred direction. When additional bars moving in the same direction were placed outside the classical receptive field (second column), the response was almost completely suppressed. However, when the outer bars moved in the opposite direction, the response was undiminished. There was no

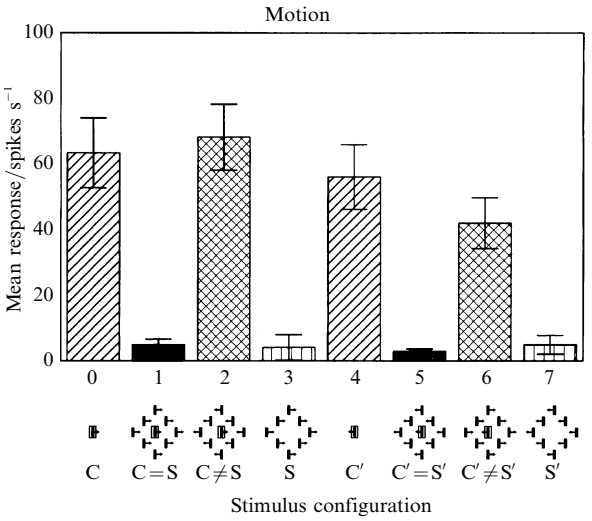


Figure 15. Neuronal response in area V1 of the cat to directional contrast. The response is strongest, when the central bar is presented alone (0) or simultaneously with a surround moving in antiphase (2). In-phase movement of the surround (1) inhibits the response. The surround by itself (3) had little effect. In the actual experiment many more bars were presented outside the receptive field. (From Kastner et al 1997.)

effect with surround motion alone. These results are consistent with the perceptual salience of the stimuli. Recent work suggests that under conditions of low salience the inhibitory centre–surround interactions for stimuli of this kind may be under the control of extensive feedback from higher areas (Bullier et al 1996; Nowak and Bullier 1997). For example, inactivation of area V2 would be expected to diminish the difference between the results for stimuli 0 and 1 on one hand, and 4 and 5 on the other.

The findings by Lamme (1995) and Kastner et al (1997) may be interpreted in terms of figure–ground segregation occurring as early as the primary visual cortex. Similar results were obtained for borders defined by luminance, colour, texture, and depth (Zipser et al 1996; for visually evoked potentials see Bach and Meigen 1997). To explain these results, long-range signals arising at the edge of the stimulus and propagated to the receptive field of the neuron are required.

3.5 *Grouping by coherent motion*

Perhaps the most powerful example of a correlation between single-cell neurophysiology and perception is perceptual grouping by coherent motion. For instance, a circle consisting of regularly spaced dots on a transparent acetate sheet cannot be discerned when superimposed onto a field of random dots, as long as both are stationary. However, as soon as the figure (or the ground) is moved, the circle is immediately perceived. This *pop-out effect* testifies to the enormous power of coherent motion as a segmentation factor. The Gestaltists would have attributed this effect to the *factor of common fate* (Wertheimer 1923; Metzger 1953).

Newsome et al (1989) reported neurons in areas V1 and MT in the behaving monkey that respond selectively to coherent motion. Such cells have very large receptive fields; and they require only 4%–7% of coherently moving dots (relative to the total number) to produce a response, even if the target dots are widely separated in space. More importantly, behavioural and neurophysiological thresholds in the same animal were the same suggesting that the behavioural response may depend on the activity of a relatively small population of neurons (Britten et al 1992).

This conclusion is made even stronger by the finding that the perceived direction of motion can be biased by electrical microstimulation of a cluster of neurons in area MT (Salzman et al 1992; Salzman and Newsome 1994). When a small group of MT neurons was stimulated, the perception of the monkey (as inferred from its behaviour) was shifted towards the motion direction preferred by this group of neurons. This study convincingly demonstrates that manipulation of a number of cortical cells is

accompanied by a correlated change in the monkey's perceived movement direction. It further suggests that area MT is crucial for movement perception.

In comparison, Peterhans and von der Heydt (1991, 1993) described neurons responding to a row of oscillating dots already in areas V2 and V3/V3A of the awake monkey. The dots were arranged collinearly and moved perpendicularly to their orientation. Two types of neurons were found: one that was highly sensitive to misalignments (as small as 2 min of arc), thus representing a collinearity detector; and another that tolerated misalignments of up to 1 deg, but was orientation-selective, ie an orientation detector. Coherent motion of the stimuli was crucial. When the dots were moved out of synchrony, the neuronal response was reduced or abolished.

Surprisingly, the neuronal response to the dotted line was comparable to or even better than the response to a continuous line defined by luminance contrast. These neurons also responded when the group of dots was moved not on a uniform background, but relative to a dotted background that was either stationary or moved in antiphase (Peterhans and von der Heydt 1989, 1991; Peterhans 1997). The authors suggest that by signalling a group of coherently moving dots on a dynamic noise background, these neurons may play an important role at an early stage of figure – ground segregation and, ultimately, in the perception of form-from-motion. Uttal et al (1999) in a psychophysical test of human observers have come to similar conclusions. In their experiment, performance was best with collinearly aligned dots moving along parallel trajectories, whereas noncollinear ('crooked') target stimuli greatly impaired detection.

3.6 *Binding by synchronisation*

Regarding the mechanism underlying coherent motion perception, one must ask how individual dots moving in the same manner are grouped together in the brain. Two research groups (Eckhorn et al 1989; Gray et al 1989) independently suggested that such 'binding' may be based on the temporal correlation in the emission of action potentials. They observed that (oscillatory) responses of cells stimulated in the same manner (ie coherently) became synchronised despite their spatial separation. Singer (1989, 1993) speculated that this kind of synchronisation might result from back-propagation (reentry) of signals from higher levels (eg MT) onto similarly tuned units at lower levels (V1), thereby linking together like-stimulus features, such as orientation, as a prerequisite for *figure – ground segregation*.

Figure 16 (from Engel et al 1992) shows schematically the receptive fields of two such cells, spaced 7 mm apart, in area 17 of the cat. Both cells have the same orientation preference as indicated by the thin vertical lines. The stimuli used were either a long continuous bar moving across both receptive fields; two short bars moving together in the same direction; or two bars moving in opposite directions. The cross-correlograms on the right show the amount of synchronisation between the neuronal responses. In the case of the continuous bar, the correlation is high. In the case of the two bars moving together, response synchronisation is reduced; and for the oppositely moving stimuli it is abolished. These findings have therefore been interpreted as a potential binding mechanism capable of grouping spatially separate elements together. These are fascinating ideas that are currently being tested in several laboratories around the world (for reviews see Tovée 1996; Engel et al 1997; Singer et al 1997).

4 How far have we come—where are we going?

The progression in vision research from simple elements to complex perceptions as discussed in this article has produced a flurry of papers on fading and filling-in, pop-out and salience, and grouping by coherent motion (for a review see Spillmann and Ehrenstein 1996). We are still far from understanding how we perceive natural scenes. However, steps are in the right direction. An important step was taken with the shift

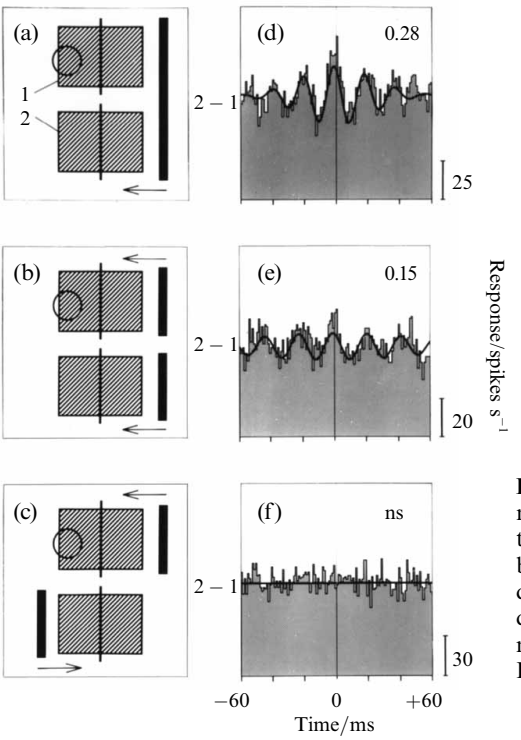


Figure 16. Left: Responses of two spatially separated neurons with the same preferred orientation in area 17 of the cat. (a) Long continuous bar; (b) two short bars moving in the same direction; (c) two short bars moving in opposite directions. Right: Synchronisation of the two neuronal responses by cross-correlation. (From Engel et al 1992.)

in paradigm from local to global perceptions (section 3). Long-distance interactions required for global perceptions were postulated in the last century by Mach (1865) and Hering (1878), while global percepts were central to the thinking of the Gestaltists (Wertheimer 1923). It is exciting to see how these early ideas are now becoming neurophysiological realities. Computational vision approaches (eg Marr 1982; Grossberg et al 1994; Grossberg and Mingolla 1985a, 1985b) have greatly contributed to this change of paradigm by providing experimentally testable hypotheses, eg potential neural solutions by context-sensitive mechanisms imparting information from contours onto adjacent surfaces.

Important questions for understanding human visual perception remain: (i) What is the significance of the multiple representation of a visual stimulus at ever higher levels and the increasing loss of retinotopic organisation (Barlow 1995)? (ii) How does the visual information analysed in the parvocellular and magnocellular streams (Livingstone and Hubel 1987, 1988) come together again?

There is now increasing evidence that individual neurons in extrastriate visual areas perform far more complex and interactive analyses than had been previously thought (Schiller and Logothetis 1990; Schiller 1997). For example, neurons in a given area may not only specialise in extracting a basic stimulus attribute such as colour; but also code depth and texture; and even engage in visual learning, spatial generalisation, and visual attention. Clearly, there is a move from the assumption of highly specific feature detectors and the modularity concept (for a review see Hubel 1988) to neurons that have multifunctional properties.

Such neurons may even have multimodal inputs to provide for an interaction between vision, on one hand; and hearing, touch, and the vestibular sense on the other (cf *sensorium commune*; Stein and Meredith 1993). Recordings were made from multimodal neurons by Freiburg researchers in the early sixties (Kornhuber 1961).

4.1 *Central questions for future research*

Other central questions that need to be answered are: How much of our perception is bottom – up, how much is top – down (Kosslyn et al 1995)? The vast majority of fibres in the optic tract of cat carries (feedback) signals from cells in area 17 to the lateral geniculate nucleus, whereas only about 10% – 20% (less than 10% in the monkey) carry (feedforward) signals from retino-geniculate afferents (Sherman and Koch 1986; Peters et al 1994; Murphy and Sillito 1996). A similar prevalence of feedback appears to exist between extrastriate areas (V2 – MT) and the primary visual cortex (Perkel et al 1986). Inactivation of any of these higher areas by local cooling drastically changes the response pattern of neurons at lower levels (Bullier et al 1996; Payne et al 1996; James et al 1997). Apparently, the visual input to any given stage ('bottom – up') is refined by a cascade of feedback circuits (Lamme et al 1997), and the question arises where does stimulus processing by feedback loops become 'top – down'.

Another important problem concerns the question of how large-scale surface properties, such as perceived transparency and depth in stratified stimulus patterns, are computed from local features (Adelson 1993; Spillmann and Werner 1996) as they must involve far more than long-range interaction between single cells. Friedman et al (1996) have recently found that many cells in area V2 of the macaque monkey respond to random-dot stereograms by signalling the edges of the cyclopean figure through edge enhancement. Cells responded maximally if the edge of the figure was centred on their receptive fields, but only weakly when the figure covered the entire receptive field. However, it remains unclear how edge extrapolation and surface stratification through smoothing and filling-in of depth planes in random-dot stereograms is achieved.

Recent research even suggests that there are 'Gestalt' cells that are largely invariant towards retinal size, position, viewpoint, even partial occlusion (Sáry et al 1993; Rolls 1994; Kovács et al 1995; Wallis and Rolls 1997). What about the role of attention and eye movements (Groner and Groner 1989; Fischer and Weber 1993; Treue and Maunsell 1996; Kastner et al 1998)? For example, is it conceivable that local enhancement of the visual field by a shift of focal attention is comparable to an eye movement that is planned, but not executed? Other important questions are: How do we coordinate a chain of glimpses of a scene into a unified percept when it moves (or when we move) behind a number of apertures such as a hedge? Specifically, how do neurons in areas MT and MSt extract biological motion (Johansson 1964; Oram and Perrett 1994) in optical flow fields (Tanaka et al 1989; Lappe et al 1996; Duffy and Wurtz 1997). Not only must we correlate stimulus (A) with that same stimulus (A′) a moment later, but we must also account for its different location.

Finally, one might ask with Miyashita (1993): Where does perception meet memory? This is currently a hot debate whether and to what degree memory (imagery) involves recruitment of visual areas, as there do not appear to be specific regions for memory (Kosslyn and Ochsner 1994; Roland and Gulyás 1994; Sakai and Miyashita 1994). Rather, memory appears to be intermingled with sensory processing areas.

These are fundamental problems in the study of vision and perception to be tackled by advanced research methods. Among them are long-term multielectrode recordings, microstimulation of nerve cell clusters, and lesion studies in trained animals. Neuroimaging techniques such as positron emission tomography or functional magnetic resonance imaging (eg Zeki 1993; Smith et al 1998) allow us to observe the human brain at work while we perceive a given stimulus, execute a given eye movement, or try to recall or imagine a visual percept. The results shed light on the relative contributions of individual brain areas to visual perception. Temporal inactivation of cortical function by transcranial magnetic stimulation (Shimojo and Kamitani 1998) complements these techniques.

It seems like a dream come true that one day one might be able to actually see dedicated nerve cells in the human brain lighting up like city lights in the dark. Never before did neuropsychologists have at their disposal such a powerful array of non-invasive research tools to identify the brain loci responsible for visual function. The steep rise in the number of publications tackling these and related issues strongly suggests that some of these questions may soon be answered for a more complete understanding of visual perception.

4.2 *Epistemological implications*

Although we are living in what is perhaps one of the most exciting periods of vision research, for some skeptics the gnawing question of an epiphenomenon remains. Yet, even to a reluctant mind, it would appear difficult to assert that the multitude of correlations between neuronal responses and perceptual phenomena described in this paper is merely coincidental. Take Grüsser's (1995) article on migraine phosphenes (ie zigzagging line segments of cortical origin resembling the fortifications of a medieval castle): Who would deny the close relationship between the presumed neuronal activity, cortical magnification, and resultant percepts? It is probably fair to say that many experiments that have furthered our understanding of the neuronal bases of visual perception would not have been performed if they had not been prompted by the firm belief that bridges (analogies) exist between single-cell activity and visual perception (eg Nelson 1985).

Uttal (1997) and others have cautioned us not to fall victim to a naive form of neuroreductionism (cf Brindley 1970; Teller 1990; Mausfeld 1996; Pessoa et al 1998). Indeed, the progression from correlation → dependence → causation → identity is logically a treacherous one. However, from a pragmatic point of view one need not worry as long as this approach continues to bear fruit. If only we agree that for two different percepts there must also be two correlated neural states, we may be safe. The goal then is to guide single-cell recordings towards biologically important problems (such as partially occluded contours) and, vice versa, focus psychophysical studies on relevant neuronal mechanisms (such as end-stopping).

It is gratifying to see that the idea of a complementary relationship between neuroanatomy, neurophysiology, and psychophysics that has marked the beginning of modern research into the visual system (Jung and Kornhuber 1961) and that has been followed up at major international conferences (Spillmann and Werner 1990; Valberg and Lee 1990) is also benefitting the *European Conference on Visual Perception*. Having enjoyed and lived through the impressive progress during that time, we are now challenged by the question: Where do visual signals become a perception? The task of the next decade is to tackle consciousness, the biggest question of all.

Acknowledgements. Preparation of this article was supported by DFG grant SP67/6-1. I thank Jean Bullier, Birgitta Dresp, Walter H Ehrenstein, Sabine Kastner, Barry Lee, Svein Magnussen, Larry Maloney, Osvaldo da Pos, Dieter Schmidt, Robert Sekuler, William Uttal, Andrea Viehöver, and John S Werner for comments and Kristian Donner for providing the impetus to write about history. The comments by two anonymous referees are appreciated. Frank Stürzel prepared figure 7.

References

Adelson E H, 1993 "Perceptual organization and the judgment of brightness" *Science* **262** 2042 – 2044

Adrian E D, Matthews R, 1927 "The action of light on the eye. I. The discharge of impulses in the optic nerve and its relation to the electrical changes in the retina" *Journal of Physiology (London)* **63** 378 – 414

Adrian E D, Matthews R, 1928 "The action of light on the eye. III. The interaction of retinal neurones" *Journal of Physiology (London)* **65** 273 – 301

Allman J, Miezin F, McGuinness E, 1985a "Stimulus specific responses from beyond the classical receptive field: Neurophysiological mechanisms for local – global comparisons in visual neurons" *Annual Review of Neuroscience* **8** 407 – 430

Allman J, Miezin F, McGuinness E, 1985b "Direction- and velocity-specific responses from beyond the classical receptive field in the middle temporal visual area (MT)" *Perception* **14** 105 – 126
Bach M, Meigen T, 1997 "Similar electrophysiological correlates of texture segregation induced by luminance, orientation, motion, and stereo" *Vision Research* **37** 1409 – 1414
Barlow H B, 1953 "Summation and inhibition in the frog's retina" *Journal of Physiology (London)* **119** 69 – 88
Barlow H B, 1972 "Single units and sensation: a neuron doctrine for perceptual psychology?" *Perception* **1** 371 – 394
Barlow H B, 1995 "The neuron doctrine in perception", in *The Cognitive Neurosciences* Ed. M Gazzaniga (Cambridge, MA: MIT Press) pp 415 – 435
Barlow H B, Derrington A M, Harris I R, Lennie P, 1977 "The effect of remote retinal stimulation on the responses of cat retinal ganglion cells" *Journal of Physiology (London)* **269** 177 – 194
Baumann R, Zwan R van der, Peterhans E, 1997 "Figure – ground segregation at contours: a neural mechanism in the visual cortex of the alert monkey" *European Journal of Neuroscience* **9** 1290 – 1303
Baumgartner G, 1960 "Indirekte Größenbestimmung der receptiven Felder der Retina beim Menschen mittels der Hermannschen Gittertäuschung" *Pflügers Archiv für die gesamte Physiologie* **272** 21 – 22
Baumgartner G, 1961 "Die Reaktionen der Neurone des zentralen visuellen Systems der Katze im simultanen Helligkeitskontrast", in *Neurophysiologie und Psychophysik des visuellen Systems* Eds R Jung, H H Kornhuber (Berlin: Springer) pp 296 – 313
Baumgartner G, 1990 "Where do visual signals become a perception?", in *The Principles of Design and Operation of the Brain* Eds J Eccles, O Creutzfeldt (Vatican: Pontificiae Academiae Scientiarum Scripta Varia) volume 78, pp 99 – 114
Baumgartner G, Heydt R von der, Peterhans E, 1984 "Anomalous contours: a tool in studying the neurophysiology of vision" *Experimental Brain Research* (supplement 9) 413 – 419
Blakemore C, Carpenter R H S, Georgeson M A, 1970 "Lateral inhibition between orientation detectors in the human visual system" *Nature (London)* **228** 37 – 39
Blakemore C, Tobin E A, 1972 "Lateral inhibition between orientation detectors in the cat's visual cortex" *Experimental Brain Research* **15** 439 – 440
Braddick O J, Campbell F W, Atkinson J, 1978 "Channels in vision: Basic aspects", in *Handbook of Sensory Physiology* volume VIII *Perception* Eds R Held, H W Leibowitz, H-L Teuber (Berlin: Springer) pp 1 – 38
Breitmeyer B, Valberg A, 1979 "Local foveal inhibitory effects of global peripheral excitation" *Science* **203** 463 – 464
Brindley G S, 1970 *Physiology of the Retina and Visual Pathways* (London: Edward Arnold)
Britten K H, Shadlen M N, Newsome W T, Movshon J A, 1992 "The analysis of visual motion: A comparison of neuronal and psychophysical performance" *Journal of Neuroscience* **12** 4745 – 4765
Bullier J, Hupé J M, James A, Girard P, 1996 "Functional interactions between areas V1 and V2 in the monkey" *Journal of Physiology (Paris)* **90** 217 – 220
Cajal S Ramon y, 1893 "La rétine des vertébrés" *La Cellule* **9** 17 – 257 [Translated by D Maguire, R W Rodieck *The Vertebrate Retina* (San Francisco, CA: Freeman, 1973)]
Creutzfeldt O D, 1990 "Brain, perception, and mind. A tribute to Richard Jung, Donald M MacKay, and Hans-Lukas Teuber", in *Visual Perception. The Neurophysiological Foundations* Eds L Spillmann, J S Werner (San Diego, CA: Academic Press) pp 449 – 463
Creutzfeldt O D, Kastner S, Xing Pei, Valberg A, 1991 "The neurophysiological correlates of colour and brightness contrast in lateral geniculate neurones II. Adaptation and surround effects" *Experimental Brain Research* **87** 22 – 45
Davey M P, Maddess T, Srinivasan M V, 1998 "The spatiotemporal properties of the Craik – O'Brien – Cornsweet effect are consistent with 'filling in'" *Vision Research* **38** 2037 – 2046
DeAngelis G C, Anzai A, Ohzawa I, Freeman R D, 1995 "Receptive field structure in the visual cortex: does selective stimulation induce plasticity?" *Proceedings of the National Academy of Sciences of the USA* **92** 9682 – 9686
De Valois R L, De Valois K K, 1990 *Spatial Vision* (New York: Oxford University Press)
De Valois R L, Webster M A, De Valois K K, Lingelbach B, 1986 "Temporal properties of brightness and color induction" *Vision Research* **26** 887 – 897
De Weerd P, Desimone R, Ungerleider L G, 1998 "Perceptual filling-in: A parametric study" *Vision Research* **38** 2721 – 2734
De Weerd P, Gattas R, Desimone R, Ungerleider L G, 1995 "Responses of cells in monkey visual cortex during perceptual filling-in of an artificial scotoma" *Nature (London)* **377** 731 – 734

Dichgans J, 1998 "Richard Jung", in *Nervenärzte – Biographien* Eds H Schliack, H Hippius (Stuttgart: G Thieme) pp 96 – 101

Dresp B, 1993 "Bright lines and edges facilitate the detection of small light targets" *Spatial Vision* **7** 213 – 225

Dresp B, 1997 "On illusory contours and their functional significance" *Current Psychology of Cognition* **16** 489 – 518

Dresp B, Bonnet C, 1995 "Subthreshold summation with illusory contours" *Vision Research* **35** 1071 – 1078

Duffy C J, Wurtz R H, 1997 "Medial superior temporal area neurons respond to speed patterns in optic flow" *Journal of Neuroscience* **17** 2839 – 2851

Eckhorn R, Bauer R, Jordan W, Brosch M, Kruse W, Munk M, Reitboeck H J, 1988 "Coherent oscillations: a mechanism of feature linking in the visual cortex? Multiple electrode and correlation analysis in the cat" *Biological Cybernetics* **60** 121 – 130

Eckhorn R, Reitboeck H J, Arndt M, Dicke P, 1989 "A neural network for feature linking via synchronous activity: results from cat visual cortex and from simulations", in *Models of Brain Function* Ed. R M J Cotterill (Cambridge: Cambridge University Press) pp 255 – 272

Ehrenstein W, 1941 "Über Abwandlungen der L. Hermannschen Helligkeitserscheinung" *Zeitschrift für Psychologie* **150** 83 – 91 ["Modifications of the brightness phenomenon of L Hermann"; translation by A Hogg, 1987, in *The Perception of Illusory Contours* Eds S Petry, G E Meyer (1987, New York: Springer) pp 35 – 39]

Ehrenstein W H, Spillmann L, 1983 "Time thresholds for increments and decrements in luminance" *Journal of the Optical Society of America* **73** 419 – 426

Engel A K, König P, Kreiter A K, Schillen T B, Singer W, 1992 "Temporal coding in the visual cortex. New vistas on integration in the nervous system" *Trends in Neurosciences* **15** 218 – 226

Engel A K, Roelfsema P R, Fries P, Brecht M, Singer W, 1997 "Role of the temporal domain for response selection and perceptual binding" *Cerebral Cortex* **7** 571 – 582

Eysel U T, Eyding D, Schweigart G, 1998 "Repetitive optical stimulation elicits fast receptive field changes in mature visual cortex" *Neuroreport* **9** 949 – 954

Eysel U T, Schweigart G, 1999 "Increased receptive field size in the surround of chronic lesions in the adult cat visual cortex" *Cerebral Cortex* **9** 101 – 109

Fechner G T, 1860 *Elemente der Psychophysik* (Leipzig: Breitkopf & Härtel)

Fiorentini A, Baumgartner G, Magnussen S, Schiller P H, Thomas J P, 1990 "The perception of brightness and darkness: Relations to neuronal receptive fields", in *Visual Perception: The Neurophysiological Foundations* Eds L Spillmann, J S Werner (San Diego, CA: Academic Press) pp 129 – 161

Fischer B, 1973 "Overlap of receptive field centers and representation of the visual field in the cat's optic tract" *Vision Research* **13** 2113 – 2120

Fischer B, Weber H, 1993 "Express saccades and visual attention" *Behavioral and Brain Sciences* **16** 553 – 610

Fox P T, Miezin F M, Allman J M, Van Essen D C, Raichle M E, 1987 "Retinotopic organization of human visual cortex mapped with positron emission tomography" *Journal of Neuroscience* **7** 913 – 922

Friedman H, Zhou H, Poggio G, Heydt R von der, 1996 "Neural mechanisms for cyclopean form perception in areas V1 and V2 of visual cortex", Fifth Teuber Symposium, MIT, Cambridge, MA, 25 – 27 October 1996 (abstract)

Fries W, Albus K, Creutzfeldt O D, 1977 "Effects of interacting visual patterns on single cell responses in cat's striate cortex" *Vision Research* **17** 1001 – 1008

Gerling J, Spillmann L, 1987 "Duration of visual afterimages on modulated backgrounds: post-receptoral processes" *Vision Research* **27** 521 – 527

Gibson J J, Radner M, 1937 "Adaptation, after-effect and contrast in the perception of tilted lines: I. Quantitative studies" *Journal of Experimental Psychology* **20** 453 – 467

Gilbert C D, 1992 "Horizontal integration and cortical dynamics" *Neuron* **9** 1 – 13

Gilbert C D, Wiesel T, 1990 "The influence of contextual stimuli on the orientation selectivity of cells in primary visual cortex of the cat" *Vision Research* **30** 1689 – 1701

Gilbert C, Wiesel T, 1992 "Receptive field dynamics in adult primary visual cortex" *Nature (London)* **356** 150 – 152

Goethe J W von, 1810 *Zur Farbenlehre* (Tübingen: J G Cotta. Diederich, Jena) [Translated by R Matthaei *Goethe's Color Theory* (New York: van Nostrand, 1971)]

Gray C M, König P, Engel A K, Singer W, 1989 "Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties" *Nature (London)* **338** 334 – 337

Gregory R L, 1987 "Illusory contours and occlusion surfaces", in *The Perception of Illusory Contours* Eds S Petry, G E Meyer (New York: Springer) pp 81 – 89
Groner R, Groner M T, 1989 "Attention and eye movement control: An overview" *European Archive of Psychiatry and Neurological Sciences* **239** 9 – 16
Grossberg S, Mingolla E, 1985a "Neural dynamics of form perception: Boundary completion, illusory figures, and neon color spreading" *Psychological Review* **92** 173 – 211
Grossberg S, Mingolla E, 1985b "Neural dynamics of perceptual grouping: Texture, boundaries, and emergent segmentation" *Perception & Psychophysics* **38** 141 – 171
Grossberg S, Mingolla E, Ross W D, 1994 "A neural theory of attentive visual search: interactions of boundary, surface, spatial, and object representations" *Psychological Review* **101** 470 – 489
Grüsser O-J, 1956 *Reaktionen einzelner corticaler und retinaler Neurone der Katze auf Flimmerlicht und ihre Beziehungen zur subjektiven Sinnesphysiologie* Dissertation, Albert-Ludwigs-Universität, Freiburg im Breisgau
Grüsser O-J, 1995 "Migraine phosphenes and the retino-cortical magnification factor" *Vision Research* **35** 1125 – 1134
Grüsser O-J, Creutzfeldt O, 1957 "Eine neurophysiologische Grundlage des Brücke – Bartley-Effektes: Maxima der Impulsfrequenz retinaler und corticaler Neurone bei Flimmerlicht mittlerer Frequenzen" *Pflügers Archiv für die gesamte Physiologie* **263** 668 – 681
Grüsser O-J, Grüsser-Cornehls U, 1973 "Neuronal mechanisms of visual movement perception and some psychophysical and behavioral correlations", in *Handbook of Sensory Physiology* volume VII/3A *Central Processing of Visual Information* Ed. R Jung (New York: Springer) pp 333 – 429
Grüsser O-J, Grüsser-Cornehls U, 1976 "Neurophysiology of the anuran visual system", in *Frog Neurobiology* Eds R Llinás, W Precht (Berlin: Springer) pp 297 – 451
Grüsser O-J, Grützner A, 1958 "Neurophysiologische Grundlagen der periodischen Nachbildphasen nach kurzen Lichtblitzen" *Graefes Archiv für Ophthalmologie* **160** 65 – 93
Hammond P, MacKay D M, 1981 "Modulatory influences of moving textured backgrounds on responsiveness of simple cells in feline striate cortex" *Journal of Physiology (London)* **319** 431 – 442
Hardage L, Tyler C W, 1995 "Induced twinkle aftereffect as a probe of dynamic visual processing mechanisms" *Vision Research* **35** 757 – 766
Hartline H K, 1938 "The response of single optic nerve fibers of the vertebrate eye to illumination of the retina" *American Journal of Physiology* **121** 400 – 415
Hartline H K, 1940 "The receptive fields of optic nerve fibers" *American Journal of Physiology* **130** 690 – 699
Hering E, 1878 "Vom simultanen Grenzkontrast", in *Zur Lehre vom Lichtsinne* (Wien: Gerold und Soehne). Also 1907 *Grundzüge der Lehre vom Lichtsinn,* in *Handbuch der gesamten Augenheilkunde* Eds Graefe-Saemisch, 2nd edition, volume 3, chapter XII (Leipzig: W Engelmann) pp 138 – 139 [Translated by L M Hurvich, D Jameson *Outlines of the Theory of the Light Sense* (Cambridge, MA: Harvard University Press, 1964)]
Hermann L, 1870 "Eine Erscheinung des simultanen Contrastes" *Pflügers Archiv für die gesamte Physiologie* **3** 13 – 15
Heydt R von der, 1987 "Approaches to visual cortical function" *Reviews of Physiology, Biochemistry and Pharmacology* **108** 69 – 151
Heydt R von der, Peterhans E, Baumgartner G, 1984 "Illusory contours and cortical neuron responses" *Science* **224** 1260 – 1262
Hofmann F B, Bielschowsky A, 1909 "Über die Einstellung der scheinbaren Horizontalen und Vertikalen bei Betrachtung eines von schrägen Konturen erfüllten Gesichtsfeldes" *Pflügers Archiv für die gesamte Physiologie* **126** 453 – 475
Holmes G, 1918 "Disturbances of vision by cerebral lesions" *British Journal of Ophthalmology* **2** 353 – 384
Hubel D H, 1988 *Eye, Brain and Vision* Scientific American Library (New York: W H Freeman)
Hubel D H, Wiesel T, 1959 "Receptive fields of single neurones in the cat's striate cortex" *Journal of Physiology (London)* **148** 574 – 591
Hubel D H, Wiesel T N, 1965 "Receptive fields and functional architecture in two nonstriate visual areas (18 and 19) of the cat" *Journal of Neurophysiology* **28** 229 – 289
James A C, Hupé J-M, Payne B R, Lomber S G, Girard P, Bullier J, 1997 "Feedback connections from area MT gate information transfer in neurons of areas V1, V2 and V3" *Society for Neuroscience* **23** 1396 (abstract)
Johansson G, 1964 "Perception of motion and changing form" *Scandinavian Journal of Psychology* **5** 181 – 207

Jung R, 1959 "Microphysiology of cortical neurons and its significance for psychophysiology" *Anales de la Facultad de Medicina, Montevideo* **44** 323 – 332

Jung R, 1961a "Neuronal integration in the visual cortex and its significance for visual information", in *Sensory Communication* Ed. W A Rosenblith (Cambridge, MA: MIT Press) pp 627 – 674

Jung R, 1961b "Korrelationen von Neuronentätigkeit und Sehen", in *Neurophysiologie und Psychophysik des visuellen Systems* Eds R Jung, H-H Kornhuber (Berlin: Springer) pp 410 – 435

Jung R, 1973 "Visual perception and neurophysiology", in *Handbook of Sensory Physiology* volume VII/3A *Central Processing of Visual Information* Ed. R Jung (Berlin: Springer) pp 1 – 152

Jung R, 1975 "Some European neuroscientists: A personal tribute", in *The Neurosciences: Paths of Discovery* Eds F G Worden, J P Swazey, G Adelman (Cambridge, MA: MIT Press) pp 477 – 511

Jung R, 1984 "Sensory research in historical perspective: philosophical foundations of perception", in *Handbook of Physiology,* Section 1 *The Nervous System* volume III/1 *Sensory Processes* Ed. I Darian-Smith (Washington, DC: American Physiological Society) pp 1 – 74

Jung R, Kornhuber H-H (Eds), 1961 *Neurophysiologie und Psychophysik des visuellen Systems* (Berlin: Springer)

Jung R, Spillmann L, 1970 "Receptive-field estimation and perceptual integration in human vision", in *Early Experience and Visual Information Processing in Perceptual and Reading Disorders* Eds F A Young, D B Lindsley (Washington, DC: National Academic Press) pp 181 – 197

Jung R, Baumgarten R von, Baumgartner G, 1952 "Mikroableitungen von einzelnėn Nervenzellen im optischen Cortex der Katze: Die lichtaktivierten B-Neurone" *Archiv für Psychiatrie und Nervenkrankheiten* **189** 521 – 539

Kaas J H, Krubitzer L A, Chino Y M, Langston A L, Polley E H, Blair N, 1990 "Reorganization of retinotopic cortical maps in adult mammals after lesions of the retina" *Science* **248** 229 – 231

Kastner S, Crook J M, Pei Xing, Creutzfeldt O D, 1992 "Neurophysiological correlates of colour induction on white surfaces" *European Journal of Neuroscience* **4** 1079 – 1086

Kastner S, De Weerd P, Desimone R, Ungerleider L G, 1998 "Mechanisms of directed attention in human ventral extrastriate cortex as revealed by functional MRI" *Science* **282** 108 – 111

Kastner S, Nothdurft H C, Pigarev I N, 1997 "Neuronal correlates of pop-out in cat striate cortex" *Vision Research* **37** 371 – 376

Knau H, Spillmann L, 1996 "Failure of brightness and color constancy under prolonged *Ganzfeld* stimulation" *SPIE Proceedings* **2657**(04) 19 – 29

Knau H, Spillmann L, 1997 "Brightness fading during *Ganzfeld* adaptation" *Journal of the Optical Society of America A* **14** 1213 – 1222

Köhler W, Held R, 1949 "The cortical correlate of pattern vision" *Science* **110** 414 – 419

Kornhuber H-H, 1961 "Convergence of vestibular, visual and auditory afferents at single neurons of the cat's cortex" *Excerpta Medica (Amsterdam) International Congress Series* **37** 11 (Abstract)

Kornhuber H-H, Spillmann L, 1964 "Zur visuellen Feldorganisation beim Menschen: Die receptiven Felder im peripheren und zentralen Gesichtsfeld bei Simultankontrast, Flimmerfusion, Scheinbewegung und Blickfolgebewegung" *Pflügers Archiv für die gesamte Physiologie* **279** R5 (Abstract)

Kosslyn S M, Ochsner K N, 1994 "In search of occipital activation during visual mental imagery" (Comment) *Trends in Neurosciences* **17** 290 – 292

Kosslyn S M, Thompson W L, Kim I J, Alpert N M, 1995 "Topographical representations of mental images in primary visual cortex" *Nature (London)* **378** 496 – 498

Kovács G, Vogels R, Orban G A, 1995 "Selectivity of macaque inferior temporal neurons for partially occluded shapes" *Journal of Neuroscience* **15** 1984 – 1997

Kovács I, Papathomas T V, Yang M, Fehér Á, 1996 "When the brain changes its mind: Interocular grouping during binocular rivalry" *Proceedings of the National Academy of Sciences of the USA* **93** 15508 – 15511

Krauskopf J, 1963 "Effect of retinal image stabilization on the appearance of heterochromatic targets" *Journal of the Optical Society of America* **53** 741 – 744

Krüger J, 1990 "Multi-microelectrode investigation of monkey striate cortex: link between correlational and neuronal properties in the infragranular layers" *Visual Neuroscience* **5** 135 – 142

Krüger J, Becker J D, 1991 "Recognizing the visual stimulus from neuronal discharges" *Trends in Neurosciences* **14** 282 – 286

Krüger J, Fischer B, 1973 "Strong periphery effect in cat retinal ganglion cells. Excitatory responses in ON- and OFF-center neurons to single grid displacements" *Experimental Brain Research* **18** 316 – 318

Kuffler S W, 1953 "Discharge patterns and functional organization of mammalian retina" *Journal of Neurophysiology* **16** 37 – 68

Lamme V, 1995 "The neurophysiology of figure – ground segregation in primary visual cortex" *Journal of Neuroscience* **15** 1605 – 1615
Lamme V A F, Zipser K, Spekreijse H, 1997 "Figure – ground signals in V1 depend on extrastriate feedback" *Investigative Ophthalmology & Visual Science* **38**(4) S969 (Abstract 4490)
Land E H, 1983 "Recent advances in retinex theory and some implications for cortical computations: color vision and the natural image" *Proceedings of the National Academy of Sciences of the USA* **80** 5163 – 5169
Lappe M, Bremmer F, Pekel M, Thiele A, Hoffmann K P, 1996 "Optic flow processing in monkey STS: a theoretical and experimental approach" *Journal of Neuroscience* **16** 6265 – 6285
Lee B B, Pokorny J, Smith V C, Martin P R, Valberg A, 1990 "Luminance and chromatic modulation sensitivity of macaque ganglion cells and human observers" *Journal of the Optical Society of America A* **7** 2223 – 2236
Lettvin J Y, Maturana H R, McCulloch W S, Pitts W H, 1959 "What the frog's eye tells the frog's brain" *Proceedings of the Institute of Radio Engineers* **47** 1940 – 1951
Levinson E, Sekuler R, 1976 "Adaptation alters perceived direction of motion" *Vision Research* **16** 779 – 781
Livingstone M S, Hubel D H, 1987 "Psychophysical evidence for separate channels for the perception of form, color, movement, and depth" *Journal of Neuroscience* **7** 3416 – 3468
Livingstone M S, Hubel D H, 1988 "Segregation of form, color, movement and depth: anatomy, physiology and perception" *Science* **240** 740 – 750
Lund J S, Yoshioka T, Levitt J B, 1993 "Comparison of intrinsic connectivity in different areas of macaque monkey cerebral cortex" *Cerebral Cortex* **3** 148 – 162
Mach E, 1865 "Über die Wirkung der räumlichen Vertheilung des Lichtreizes auf die Netzhaut, I" *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Wien, Mathematisch-Naturwissenschaftliche Classe, Zweite Abteilung* **52** 303 – 322
McIlwain J T, 1964 "Receptive fields of optic tract axons and lateral geniculate cells. Peripheral extent and barbiturate sensitivity" *Journal of Neurophysiology* **27** 1154 – 1173
Maffei L, Fiorentini A, 1976 "The unresponsive regions of visual cortical receptive fields" *Vision Research* **16** 1131 – 1139
Magnussen S, Glad A, 1975a "Brightness and darkness enhancement during flicker: Perceptual correlates of neuronal B- and D-systems in human vision" *Experimental Brain Research* **22** 399 – 413
Magnussen S, Glad A, 1975b "Temporal frequency characteristics of spatial interaction in human vision" *Experimental Brain Research* **23** 519 – 528
Magnussen S, Kurtenbach W, 1980a "Linear summation of tilt illusion and tilt aftereffect" *Vision Research* **20** 39 – 42
Magnussen S, Kurtenbach W, 1980b "Adapting to two orientations: Disinhibition in a visual after-effect" *Science* **207** 908 – 909
Marcar V L, Xiao D K, Raiguel S E, Maes H, Orban G A, 1995 "Processing of kinetically defined boundaries in the cortical motion area MT of the macaque monkey" *Journal of Neurophysiology* **74** 1258 – 1270
Marr D, 1982 *Vision: A Computational Investigation into the Human Representation and Processing of Visual Information* (San Francisco, CA: Freeman)
Mausfeld R, 1996 "Wahrnehmung" (perception), in *Wörterbuch der Kognitionswissenschaft* Ed. G Strube (Stuttgart: Klett-Cotta) pp 776 – 792
Metzger W, 1953 *Gesetze des Sehens* 2nd edition (Frankfurt am Main: Waldemar Kramer)
Metzger W, 1961 "Aporien der Psychophysik", in *Neurophysiologie und Psychophysik des visuellen Systems* Eds R Jung, H-H Kornhuber (Berlin: Springer) pp 435 – 444
Miyashita Y, 1993 "Inferior temporal cortex: Where perception meets memory" *Annual Review of Neuroscience* **16** 245 – 263
Munk M H J, Nowak L G, Nelson J I, Bullier J, 1995 "Structural basis of cortical synchronization. II. Effects of cortical lesions" *Journal of Neurophysiology* **74** 2401 – 2414
Murphy P C, Sillito A M, 1996 "Functional morphology of the feedback pathway from area 17 of the cat visual cortex to the lateral geniculate nucleus" *Journal of Neuroscience* **16** 1180 – 1192
Nelson J I, 1985 "The cellular basis of perception", in *Models of the Visual Cortex* Eds D Rose, V Dobson (Chichester, Sussex: John Wiley and Sons) pp 108 – 122
Nelson J I, Frost B J, 1978 "Orientation-selective inhibition from beyond the classic visual receptive field" *Brain Research* **139** 359 – 365
Nelson R, Famiglietti E V, Kolb H, 1978 "Intracellular staining reveals different levels of stratification for on- and off-center ganglion cells in cat retina" *Journal of Neurophysiology* **41** 472 – 483

Neumeyer C, Spillmann L, 1977 "Fading of steadily fixated large test fields in extrafoveal vision" *Pflügers Archiv* **368** R40 (Abstract)
Newsome W T, Britten K H, Movshon J A, 1989 "Neuronal correlates of a perceptual decision" *Nature (London)* **341** 52 – 54
Nowak L G, Bullier J, 1997 "The timing of information transfer in the visual system", in *Cerebral Cortex* volume 12, chapter 5 Eds K S Rockland, J H Kaas, A Peters (New York: Plenum) pp 205 – 241
Oram M W, Perrett D I, 1994 "Responses of anterior superior temporal polysensory (SPa) neurons to 'biological motion' stimuli" *Journal of Cognitive Neuroscience* **6** 99 – 116
Paradiso M A, Hahn S, 1996 "Filling-in percepts produced by luminance modulation" *Vision Research* **36** 2657 – 2663
Paradiso M A, Kim W, Nayak S, 1996 "Cortical representation of surface brightness: influences from beyond the classical receptive field" *Society for Neuroscience* **22** 951 (Abstract 376.6.)
Paradiso M A, Nakayama K, 1991 "Brightness perception and filling-in" *Vision Research* **31** 1221 – 1236
Payne B R, Lomber S G, Villa A E, Bullier J, 1996 "Reversible deactivation of cerebral network components" *Trends in Neurosciences* **19** 535 – 542
Perkel D J, Bullier J, Kennedy H, 1986 "Topography of the afferent connectivity of area 17 of the macaque monkey: a double-labelling study" *Journal of Comparative Neurology* **253** 374 – 402
Pessoa L, Thompson E, Noe Alva, 1998 "Finding out about filling in: a guide to perceptual completion for visual science and the philosophy of perception" *Behavioral and Brain Sciences* **21** 723 – 747
Peterhans E, 1997 "Functional organization of area V2 in the awake monkey", in *Cerebral Cortex* volume 12, chapter 8 *Extrastriate Cortex in Primates* Eds K S Rockland, J H Kaas, A Peters (New York: Plenum) pp 335 – 357
Peterhans E, Heydt R von der, 1989 "The whole and the pieces—cortical neuron responses to bars and rows of moving dots", in *Seeing Contours and Colour* Eds J J Kulikowski, C M Dickinson, I J Murray (Oxford: Pergamon Press) pp 125 – 130
Peterhans E, Heydt R von der, 1991 "Elements of form perception in monkey prestriate cortex", in *Representations of Vision: Trends and Tacit Assumptions in Vision Research* Eds A Gorea, Y Frégnac, Z Kapoula, J Findlay (Cambridge: Cambridge University Press) pp 111 – 124
Peterhans E, Heydt R von der, 1993 "Functional organization of area V2 in the alert macaque" *European Journal of Neuroscience* **5** 509 – 524
Peterhans E, Heydt R von der, Baumgartner G, 1982 "Cortical neuron responses and 'illusory' contours" *Perception* **11**(1) A19 (Abstract)
Peters A, Payne B R, Budd J A, 1994 "A numerical analysis of the geniculocortical input to striate cortex in the monkey" *Cerebral Cortex* **3** 69 – 78
Poppelreuter W, 1917 *Die Störungen der niederen und höheren Sehleistungen durch Verletzungen des Okzipitalhirns* (Leipzig: L Voss); [Translated by J Zihl, L Weiskrantz *Disturbances of Lower and Higher Visual Capacities Caused by Occipital Damage* (Oxford: Clarendon Press, 1990)]
Przybyszewski A W, 1997 "Overview of Otto-Joachim Grüsser's work" *Biological Cybernetics* **76** 317 – 320
Rabelo C, Grüsser O-J, 1961 "Die Abhängigkeit der subjektiven Helligkeit intermittierender Lichtreize von der Flimmerfrequenz (Brücke-Effekt, 'brightness enhancement'): Untersuchungen bei verschiedener Leuchtdichte und Feldgröβe" *Psychologische Forschung* **26** 299 – 312
Ramachandran V S, Gregory R L, 1991 "Perceptual filling in of artificially induced scotomas in human vision" *Nature (London)* **350** 699 – 702
Ransom-Hogg A, Spillmann L, 1980 "Perceptive field size in fovea and periphery of the light- and dark-adapted retina" *Vision Research* **20** 221 – 228
Ratliff F, 1965 *Mach Bands: Quantitative Studies on Neural Networks in the Retina* (San Francisco, CA: Holden-Day)
Rodieck R W, 1965 "Quantitative analysis of cat retinal ganglion cell response to visual stimuli" *Vision Research* **5** 583 – 601
Roland P E, Gulyás B, 1994 "Visual imagery and visual representation" *Trends in Neurosciences* **17** 281 – 287
Rolls E T, 1994 "Brain mechanisms for invariant visual recognition and learning" *Behavioural Processes* **33** 113 – 138
Rosenblith W A (Ed.), 1961 *Sensory Communication* (Cambridge, MA: MIT Press)
Rossi A F, Paradiso M A, 1996 "Temporal limits of brightness induction and mechanisms of brightness perception" *Vision Research* **36** 1391 – 1398

Rossi A F, Rittenhouse C D, Paradiso M A, 1996 "The representation of brightness in primary visual cortex" *Science* **273** 1104 – 1107
Safran A B, Landis T, 1996 "Plasticity in the adult visual cortex: implications for the diagnosis of visual field defects and visual rehabilitation" *Current Opinion in Ophthalmology* **7** 53 – 64
Sakai K, Miyashita Y, 1994 "Visual imagery: an interaction between memory retrieved and focal attention" (Comment) *Trends in Neurosciences* **17** 287 – 289
Salzman C D, Murasugi C M, Britten K H, Newsome W T, 1992 "Microstimulation in visual area MT: Effects on direction discrimination performance" *Journal of Neuroscience* **12** 2331 – 2355
Salzman C D, Newsome W T, 1994 "Neural mechanisms for forming a perceptual decision" *Science* **264** 231 – 237
Sáry G, Vogels R, Orban G A, 1993 "Cue-invariant shape selectivity of macaque inferior temporal neurons" *Science* **260** 995 – 997
Schiller P H, 1982 "Central connections on the retinal ON and OFF pathways" *Nature (London)* **297** 580 – 583
Schiller P H, 1997 "Past and present ideas about how the visual scene is analyzed by the brain", in *Cerebral Cortex* volume 12, chapter 8 *Extrastriate Cortex in Primates* Eds K S Rockland, J H Kaas, A Peters (New York: Plenum) pp 59 – 87
Schiller P H, Logothetis N K, 1990 "The color-opponent and broadband channels of the primate visual system" *Trends in Neurosciences* **13** 392 – 398
Schiller P H, Sandell J H, Maunsell J H R, 1986 "Functions of the ON and OFF channels of the visual system" *Nature (London)* **322** 824 – 825
Schmidt K E, Goebel R, Loewel S, Singer W, 1997 "The perceptual grouping criterion of colinearity is reflected by anisotropies of connections in the primary visual cortex" *European Journal of Neuroscience* **9** 1083 – 1089
Schober H, Rentschler I, 1972 *Das Bild als Schein der Wirklichkeit* (München: Heinz Moos)
Schwartz E L, 1984 "Spatial mapping and spatial vision in primate striate and infero-temporal cortex", in *Sensory Experience, Adaptation, and Perception* Eds L Spillmann, B R Wooten (Hillsdale, NJ: Lawrence Erlbaum Associates) pp 73 – 104
Schwartz E L, 1994 "Topographical mapping in primate visual cortex: history, anatomy and computation", in *Visual Science and Engineering: Models and Applications* Ed. D H Kelly (New York: Marcel Dekker) pp 293 – 359
Sekuler R, Blake R (Eds), 1994 *Perception* third edition (New York: McGraw-Hill)
Sherman S M, Koch C, 1986 "The control of retinogeniculate transmission in the mammalian lateral geniculate nucleus" *Experimental Brain Research* **63** 1 – 20
Shimojo S, Kamitani Y, 1998 "Visualizing suppression induced by transcranial magnetic stimulation. (II) Anisotropy of suppression in oriented patterns" *Investigative Ophthalmology & Visual Science* **39**(4) S672 (Abstract 3094)
Sillito A M, Grieve K L, Jones H E, Cudeiro J, Davis J, 1995 "Visual cortical mechanisms detecting focal orientation discontinuities" *Nature (London)* **378** 492 – 496
Singer W, 1989 "Search for coherence: A basic principle of cortical self-organization" *Concepts in Neuroscience* **1** 1 – 25
Singer W, 1993 "Synchronization of cortical activity and its putative role in information processing and learning" *Annual Review of Physiology* **55** 349 – 374
Singer W, Engel A K, Kreiter A K, Munk M H J, Neuenschwander S, Roelfsema P R, 1997 "Neuronal assemblies: necessity, significance, and detectability" *Trends in Cognitive Sciences* **1** 252 – 261
Smith A T, Greenlee M W, Singh K D, Kraemer F M, Hennig J, 1998 "The processing of first- and second-order motion in human visual cortex assessed by functional magnetic resonance imaging (fMRI)" *Journal of Neuroscience* **18** 3816 – 3830
Soriano M, Spillmann L, Bach M, 1996 "The abutting grating illusion" *Vision Research* **36** 109 – 116
Spillmann L, 1971 "Foveal perceptive fields in the human visual system measured with simultaneous contrast in grids and bars" *Pflügers Archiv für die gesamte Physiologie* **326** 281 – 299
Spillmann L, 1994 "The Hermann grid illusion: A tool for studying human perceptive field organization" *Perception* **23** 691 – 708
Spillmann L, Dresp B, 1995 "Phenomena of illusory form: Can we bridge the gap between levels of explanation?" *Perception* **24** 1333 – 1364
Spillmann L, Ehrenstein W H, 1996 "From neuron to Gestalt-mechanisms of visual perception", in *Comprehensive Human Physiology. From Cellular Mechanisms to Integration* chapter 43, Eds R Greger, U Windhorst (Heidelberg: Springer) pp 861 – 893

Spillmann L, Kurtenbach A, 1992 "Dynamic noise backgrounds facilitate target fading" *Vision Research* **32** 1941 – 1946
Spillmann L, Ransom-Hogg A, Oehler R, 1987 "A comparison of perceptive and receptive fields in man and monkey" *Human Neurobiology* **6** 51 – 62
Spillmann L, Werner J S (Eds), 1990 *Visual Perception. The Neurophysiological Foundations* (San Diego, CA: Academic Press)
Spillmann L, Werner J S, 1996 "Long-range effects in visual perception" *Trends in Neurosciences* **19** 428 – 434
Stein B E, Meredith M A (Eds), 1993 *The Merging of the Senses* (Cambridge, MA: MIT Press)
Sumi S, Noguchi K, 1996 *New Horizons in the Study of Gestalt Perception* (reprinted from *Japanese Psychological Research* volumes 36 and 37; distributed gratis by S Sumi, Psychology Laboratory, Keio University, Hiyoshi, Yokohama 223, Japan), p. 111
Szily A von, 1918 *Atlas der Kriegsaugenheilkunde, samt begleitendem Text* volume 1 (Stuttgart: Enke)
Tanaka K, Fukada Y, Saito H, 1989 "Underlying mechanisms of the response specificity of expansion/contraction and rotation cells in the dorsal part of the medial superior temporal area of the monkey" *Journal of Neurophysiology* **62** 642 – 656
Teller D Y, 1990 "The domain of visual science", in *Visual Perception. The Neurophysiological Foundations* Eds L Spillmann, J S Werner (San Diego, CA: Academic Press) pp 11 – 21
Teuber H-L, 1967 "Wolfgang Köhler 1887 – 1967" *Psychologische Forschung* **31** VI – XVI
Teuber H-L, Battersby N S, Bender M F, 1960 *Visual Field Defects after Penetrating Missile Wounds of the Brain* (Cambridge, MA: Harvard University Press)
Tononi G, Sporns O, Edelman G M, 1992 "Reentry and the problem of integrating multiple cortical areas: simulation of dynamic integration in the visual system" *Cerebral Cortex* **2** 310 – 335
Tootell R, Silverman M, Switkes E, De Valois R L, 1982 "Deoxyglucose analysis of retinotopic organization in primate striate cortex" *Science* **218** 902 – 904
Tovée M J, 1996 *An Introduction to the Visual System* (Cambridge: Cambridge University Press) pp 169 – 179
Treue S, Maunsell J H, 1996 "Attentional modulation of visual motion processing in cortical areas MT and MST" *Nature (London)* **382** 539 – 541
Ts'o D Y, Gilbert C D, Wiesel T N, 1986 "Relationships between horizontal interactions and functional architecture in cat striate cortex as revealed by cross-correlation analysis" *Journal of Neuroscience* **6** 1160 – 1170
Tyler C W, Hardage L, 1998 "Long-range twinkle induction: An achromatic rebound effect in the magnocellular processing system?" *Perception* **27** 203 – 214
Uttal W R, 1997 "Do theoretical bridges exist between perceptual experience and neurophysiology?" *Perspectives in Biology and Medicine* **40** 280 – 302
Uttal W R, Spillmann L, Sekuler A B, 1999 "Motion and shape in common fate" *Vision Research* (accepted pending revisions)
Valberg A, Lee B B (Eds), 1990 *From Pigments to Perception—Advances in Understanding Visual Processes* NATO ASI Series A, volume 203 (New York: Plenum)
Valberg A, Lee B B, Tigwell D A, Creutzfeldt O D, 1985 "A simultaneous contrast effect of steady remote surrounds on responses of cells in macaque lateral geniculate nucleus" *Experimental Brain Research* **58** 604 – 608
Valberg A, Spillmann L, 1982 "Foveal inhibition and facilitation caused by remote grating jerks: Interaction between long-range and short-range effects" *Experimental Brain Research* **46** 89 – 98
Van Essen D C, Felleman D J, DeYoe E A, Knierim J J, 1991 "Probing the primate visual cortex: pathways and perspectives", in *From Pigments to Perception—Advances in Understanding Visual Processes* Eds A Valberg, B B Lee (New York: Plenum) pp 227 – 237
Wallis G, Rolls E T, 1997 "Invariant face and object recognition in the visual system" *Progress in Neurobiology* **51** 167 – 194
Wässle H, Peichl L, Boycott B B, 1981 "Morphology and topography of on- and off-alpha cells in the cat retina" *Proceedings of the Royal Society of London, Series B* **212** 157 – 175
Wertheimer M, 1923 "Untersuchungen zur Lehre von der Gestalt II" *Psychologische Forschung* **4** 301 – 350
Westheimer G, 1965 "Spatial interaction in human cone vision" *Journal of Physiology (London)* **181** 881 – 894
Witkin H A, 1959 "The perception of the upright?" *Scientific American* **200** 51 – 70
Wohlfarth E, 1932 "Der Auffassungsvorgang an kleinen Gestalten. Zur Psychologie der Vorgestalterlebnisses" *Neue Psychologische Studien* **4** 347 – 414
Wolfe J, 1984 "Global factors in the Hermann grid illusion" *Perception* **13** 33 – 40

Wolfson S S, Landy M S, 1998 "Long-range interactions between texture elements" *Investigative Ophthalmology & Visual Science* **39**(4) S650 (Abstract 3018)
Wundt W, 1911 *Grundzüge der physiologischen Psychologie* volume 3, 6th edition (Leipzig: W Engelmann)
Yu C, Essock E A, 1996 "Psychophysical end-stopping associated with line targets" *Vision Research* **36** 2883 – 2896
Yu C, Levi D M, 1997 "End-stopping and length tuning in psychophysical spatial filters" *Journal of the Optical Society of America A* **14** 2346 – 2354
Zeki S M, 1983 "Colour coding in the cerebral cortex: The response of wavelength-selective and colour-coded cells in monkey visual cortex to changes in wavelength composition" *Neuroscience* **9** 767 – 781
Zeki S M, 1993 *A Vision of the Brain* (Oxford: Blackwell Scientific)
Zipser K, Lamme V A F, Schiller P H, 1996 "Contextual modulation in primary visual cortex" *Journal of Neurophysiology* **16** 7376 – 7389