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Vision Research

Minireview

Phenomenology and neurophysiological correlations: Two approaches to perception research ☆

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A R T I C L E   I N F O

A B S T R A C T

This article argues that phenomenological description and neurophysiological correlation complement each other in perception research. Whilst phenomena constitute the material, neuronal mechanisms are indispensable for their explanation. Numerous examples of neurophysiological correlates show that the correlation of phenomenology and neurophysiology is fruitful. Phenomena for which neuronal mechanism have been found include: (in area V1) filling-in of real and artificial scotomata, contour integration, figure-ground segregation by orientation contrast, amodal completion, and motion transparency; (in V2) modal completion, border ownership, surface transparency, and cyclopean perception; (in V3) alignment in dotted contours, and filling-in with dynamic texture; (in V4) colour constancy; (in MT) shape by accretion/deletion, grouping by coherent motion, apparent motion in motion quartets, motion in apertures, and biological motion. Results suggest that in monkey visual cortex, occlusion cues, including stereo depth, are predominantly processed in lower areas, whereas mechanisms for grouping and motion are primarily represented in higher areas. More correlations are likely to emerge as neuroscientists strive for a better understanding of visual perception. The paper concludes with a review of major achievements in visual neuroscience pertinent to the study of the phenomena under consideration.

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1. Introduction

> *Why do things look as they do?*   Kurt Koffka, 1935

There are two major approaches to the study of visual perception. One emphasises phenomenology as a method for describing phenomena and collecting data. It maintains that phenomena should be explained only by observable facts, i.e., in relation to other phenomena (Bozzi, 1989; Bozzi, 1999; Da Pos, 2002, 2008). This approach derives historically from the work of Brentano, Stumpf, and Bühler and has been the method of choice, for example, in Padova and Trieste (for review see Albertazzi, 1992/1993).

The other approach advocates that phenomenology must be supported by neurophysiology to explain a given phenomenon (Jung, 1973); it thereby transcends the boundaries of phenomenology. This approach has its roots in the psychophysical parallelism of Purkinje, Mach, and Hering and was most clearly enunciated, for example, by the Freiburg School of Neurophysiology and similar pursuits in Cambridge, Pisa, and Zurich.

The scientific aim of the first approach is to discover and describe structural laws of visual experience by the systematic and controlled variation of a phenomenon by an independent variable (Sinico, 2003). For example, the induction of illusory contours in the Kanizsa triangle could be studied as a function of the inducers' separation, alignment or curvature. In this way the boundary conditions for the occurrence of a given phenomenon can be defined. This discipline is primarily European (Gilchrist, 1996; Zanforlin, 2004).

The thrust of the second approach is expressed in the title of the Freiburg conference on the *Psychophysics and Neurophysiology of the Visual System* (Jung & Kornhuber, 1961); and the follow-up conference on *The Neurophysiological Foundations of Visual Perception* in Badenweiler (Spillmann & Werner, 1990). This approach also started out as a European endeavour, e.g., the discovery of the brightness and darkness systems in the cat visual cortex (Jung, Baumgarten, & von Baumgartner, 1952; Baumgartner, 1961; Jung, 1961b), before it was embraced by researchers in other parts of the world (e.g., Cambridge/MA, Boston, Berkeley, Canberra).

Is there a way to reconcile these two approaches? A useful distinction between the phenomenological and neurophysiological approaches holds that one of them aims at what vision is *like*, i.e., description, whereas the other focuses at what vision is *for* and how it *comes about*, i.e., explanation.[1]

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[1] Tse (personal communication): an analogous distinction exists in the field of biology between *Linnaean* taxonomy and modern genetics. The former is descriptive and looks for structure and relationships among species, the latter analyses similarities and dissimilarities in terms of their causal origins.

Terminological and philosophical questions have arisen from this dichotomy, specifically what phenomenology means in this context, what one should accept as an explanation of a phenomenon, and whether reductionism is the only possible scientific tenet (Sinico, 2003).

Here, I present arguments for the fruitfulness of pursuing complementary strategies by correlating phenomenological observations with psychophysical measurements and neurophysiological recordings. This is done in the hope that a deeper understanding of visual perception may be obtained by using a combined approach. Let us look at the two different strategies in perspective.

2. Phenomenology

Phenomenology encompasses the careful, unbiased description of our perceptual experience as well as its formal conceptualisation in terms of rules or "laws," sometimes encoded in mathematical models.

Good phenomenology suggests the underlying processes and their interrelations. For example, in the Hornbostel effect (1922), a rotating wire-outline cube, subject to perceptual ambiguity, is perceived to undergo depth reversal and size distortion (Nelson, 1975). Accordingly, the "near" face of the cube whose position is erroneously seen as "up front", has a retinal image that is small, and as a consequence the cube is perceived to have a trapezoidal shape, overruling higher-order cognitive knowledge. We can infer that the output of one cue system (depth) is the input to another (e.g., reversed direction of rotation, size–distance scaling, plastic deformation). In other words, a false perceptual organisation in one system produces nonveridical percepts in others. Thus, phenomenology reveals the flow of information and the underlying "wiring" between the various cue systems.

Other well-known examples within the phenomenological realm include studies of the stereokinetic effect, surface transparency, and brightness enhancement. In this role, phenomenology is of key importance not only to the understanding of perception, but also to art and design (cf. Arnheim, 1954/1974). Furthermore, many applied sciences and technologies, such as architecture, communication, graphics, colorimetry, and virtual reality will benefit from careful and systematic observation.

Although the descriptive role of phenomenology is well accepted, the explanatory side of it is controversial. Do demonstrations qualify as explanations? The answer depends on which camp one is in. For some, a demonstration is just a visualisation of an effect; for others, it is scientific proof, as one cannot decide whether a given event is the cause of, or simply the condition for, another event. Importantly, explanations must be logically consistent and have predictive power by virtue of induction and deduction. In other words, hypotheses must be testable and should lead to new experimental results.

Students of perception have long known that there is no unique relationship between a stimulus and its percept. The same stimulus can elicit different perceptions (changes in surround properties may affect brightness, hue, and saturation); conversely, the same percept can emerge from different stimuli (identical motion percepts may arise from real motion and induced motion; cf. Duncker, 1929). Here, appearance tells us something about context-dependency and structural organisation of a stimulus embedded within a surround, or a scene, that must be built into the underlying mechanisms to account for such phenomena.

The aim of phenomenology and its unifying achievement thus is to derive organisational principles of visual perception from observable facts, without recourse to physics, neurophysiology, or higher cognitive processes (Da Pos, 2002). This concept found its clearest expression in Gestalt psychology, which proposed laws of perception based entirely on phenomena (e.g., Wertheimer, 1923; Metzger, 1936/2006). By looking at the figures illustrating a given phenomenon, observers can see for themselves what is being described, and there is no need for further proof. This is one of the reasons why phenomenologists consider physiological explanations as reductionistic, inadequate, and unnecessary. Yet, the early Gestaltists did not exclude a physiological base of perception as is evident from Wertheimer's (1912) interpretation of the phi-phenomenon (apparent motion) in terms of a cerebral short-circuit (*Querfunktion*). Köhler (1920) and Köhler and Held (1949) seeking the cortical correlate of pattern vision even went further by associating perceptual Gestalten with *physische Gestalten* (physical Gestalten) and isomorphic electro-chemical fields in the brain.

In 1946, Köhler attempted to alter the perceived position of contours in the figural after-effect by applying voltage to electrodes attached to the head (J.I. Nelson, personal communication). Hans Wallach and Michael Wertheimer were among his subjects. It did not work; the perceived position of the contours was unaffected. Whilst today we know that transcranial magnetic stimulation would be a more effective probe than Köhler's crude surface electrodes, such attempts reveal that the early phenomenologists were in search of the neural underpinnings of the perceptions under consideration.

3. The primacy of perception

A great gift of phenomenology to visual science is the insight that what comes first in perception research is careful observation. To come up with a perceptual effect, one first has to *see* it. Phenomenologists discover new relationships and frequently entirely new perceptual effects because they are keen observers. Not all perceptual phenomena, of course, are as conspicuous as the masterful illustrations by Kanizsa (1979), an artist himself, for whom demonstrations sufficed.

Clearly, observing is a skill that requires not just an open eye, but also an unbiased mind, ready to notice what had not been noticed before. Artists are adept in this kind of skill; so are experimental phenomenologists. For example, over many years, Cesare Musatti, Fabio Metelli, Gaetano Kanizsa, Paolo Bozzi, and Giovanni Vicario met with their followers in Medana, Slovenia, for informal discussions of interesting and puzzling phenomena. In this way the smallest facet took on an importance as it may have revealed an unexpected insight into the nature of a given phenomenon.

These scientists and others around the world (e.g., in Germany, Belgium, Sweden, and Japan) had been trained to open their eyes and wait for visual stimuli to "speak" to them. By specifying the figural, chromatic, and dynamic conditions for a given phenomenon, they provided the framework for later research and theory. Metzger's (1934) description of the *Ganzfeld*, Kanizsa's (1955, 1979) demonstrations of illusory contours, Metelli's (1974) laws of transparency as well as Musatti's (1924) constraints of the stereokinetic effect, Michotte's 1946/1963) modes of apparent causality, and Johansson's (1973) demonstration of biological motion – they all arose from such an attempt. With few exceptions, the question of a neuronal origin of these phenomena was not asked by these researchers and, at the time, was not required; yet the later impact on cortical neurophysiology proved powerful and productive.

4. The role of illusions in perception

Among puzzling phenomena visual illusions stand out as prime examples. Why are illusions of interest to perception researchers? The answer is that illusions are percepts that belie our knowledge of the stimulus, but at the same time enable us to study the mech-

anisms and processes underlying our daily perceptions. Epistemologically, illusions are nonveridical percepts that reveal the processes by which veridical perception mediates our representation of the visual world. In this sense illusions are exceptions to the expectation that perception faithfully reflects the stimulus at the level of the retina (i.e., naïve realism). Or, as one might put it, they show the brain's signature superimposed upon the stimulus.

Aside from representing the world around us, perception also strives to maintain stability of our visual environment. As we turn our head, move our eyes, and navigate, it takes neuronal mechanisms powerful enough to give us veridical vision in real time based on inputs that are seldom complete or stable. Without these compensations, we would be seeing images that are out of register and incoherent, preventing us from getting around and ever reaching a target. The flash-lag effect (Nijhawan, 1994), demonstrating the delay between the physical and perceptual timing of an event, is an excellent example of what can go wrong if the individual glimpses during an eye movement are not properly updated and put together.

Academic enterprises aimed at promoting the scientific study of illusions started in 1993, when a Study Group on Visual Illusions and Effects (VIAE), working inside the International Colour Association (AIC), presented their results at the Göteborg AIC Interim Meeting; and, even more visibly, at the 15th AIC Congress in Kyoto, when a special session was dedicated to the analysis of colour illusions (Da Pos, 1997). More recently, other scientific enterprises have emerged, for example, a session chaired by Richard Gregory on illusory effects at the *Science Museum* in Glasgow (ECVP, 2004); and starting a year later, "*The Best Visual Illusion of the Year Contest*" http://www.illusioncontest.neuralcorrelate.com, organised by Susana Martinez-Conde, Steve Macknik, and Peter Tse.

This highly popular and most enjoyable contest began at the *European Conference on Visual Perception* in A Coruña (2005) and is now hosted by the annual convention of the *Vision Science Society*. The contest has instilled tremendous enthusiasm in the vision community, not the least because it awards prizes for the best illusions. Entries are preselected according to their significance for the understanding of the visual system. Some of the more striking phenomena presented at the contest have been described and published in the premier journals in our field; a number have even made it into research papers (e.g., Gori & Stubbs, 2006). Thus, the contest fills a double purpose by fostering fresh research and bringing visual science to public awareness.

A new permanent exhibit on visual illusions has recently been opened at the *Fleischmann Planetarium* and *Science Museum* at the University of Nevada, Reno. The exhibit was funded by a grant from the *Optical Society of America* and was formally opened with a lecture by Stuart Anstis entitled "Illusions are not what they seem." Earlier well-known exhibits – some temporary, some permanent – include those at the *Exploratorium* in San Francisco, *Phenomena* in Zurich, the *British Museum*, the *Hands-on-Museum* in Bristol, *Technorama* in Winterthur, and *Turm der Sinne* in Nuremberg, among others. Bernd Lingelbach features a remarkable collection of life-sized visual displays in a barn near his home in Aalen.

Although such centres do not instantly make every visitor into a trained phenomenologist, they alert people – predominantly young audiences – to the wonders of perception and show them how science can be fun. In this way, visitors leave with an awakened curiosity and a confirmed pleasure in searching for information for themselves. All of these activities attest to the important role phenomenology is enjoying in vision research. The proceedings of a recent conference on *Experimental Phenomenology* in Milan will be published in Teorie and Modelli (2008). Useful websites displaying a host of visual illusions, some of them interactive, can be found on the internet.

5. Neurophysiological correlates of visual perception

How about the other approach to perception, the study of the neuronal underpinnings? The need for an integrated approach to perceptual research based on the phenomenology, psychophysics, and neurophysiology of vision may sound like a truism today, but when this approach was first started some 50 years ago, it was revolutionary (see Spillmann, 1999).

Peter Schiller once remarked that, following the pioneering studies by Hartline, Kuffler, and Mountcastle, the Freiburg conference on the *Psychophysics and Neurophysiology of the Visual System* (Jung & Kornhuber, 1961) marked the beginning of a new line of studies on vision and perception, as did the MIT conference on *Sensory Communication* (Rosenblith, 1961). Within one decade, numerous phenomena and effects described within the course of a hundred years' of subjective sensory physiology became correlated with their possible neuronal counterparts (see Table 2 in Jung, 1973, pp. 28/29). These advances were largely based on spike-count responses obtained from microelectrode recordings of individual neurones.

An example is the correlation between the phenomena of border and inner contrast (*Binnenkontrast*) and their respective neuronal response patterns. Fig. 1 illustrates the impulse profile for a white bar on a black background. The peaks and trough of the response pattern closely reflect the distribution of brightness and darkness across the bar. It is highly implausible that the correlation comes about by coincidence.

The neurophysiological strategy that evolved from this approach assumed that all conscious visual experience has a neural basis, although not every neural process has a phenomenological counterpart (for examples see Spillmann & Werner, 1990). The aim of this kind of research then is to correlate a phenomenon with its putative neural mechanism.
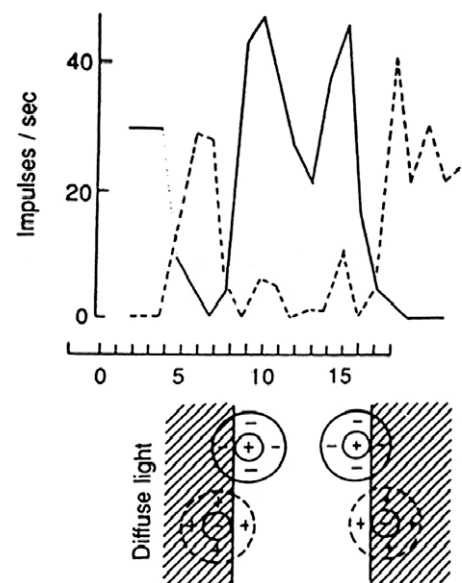

Fig. 1. Border contrast and inner contrast as reflected by neuronal firing rates. The impulse rate recorded from the optic nerve of the cat is plotted as a function of stimulus position (abscissa) relative to the receptive field. The stimulus was a white bar that was moved across the receptive field in discrete steps. The continuous curve refers to a B-neurone (for brighter), the dashed curve to a D-neurone (for darker). Response maxima signal brightness and darkness enhancement, respectively, corresponding to border contrast. The trough in the middle corresponds to inner contrast (from Baumgartner, quoted by Baumgartner & Hakas, 1962; Jung, 1961a).

This research is consistent with functional isomorphism (Scheerer, 1994), where the neural correlate of a perceptual phenomenon, which we are able so far to document, is part of the neurophysiological explanation of the subjective percept. Illuminating examples of this approach include studies of the Hermann grid illusion (for review see Spillmann, 1994; for alternative interpretations Schiller & Carvey, 2005; Geier, Bernáth, Hudák, & Séra, 2008; Levine & McAnany, 2008), the Ehrenstein illusion (Von der Heydt & Peterhans, 1989a), the neon colour effect (for review see Bressan, Mingolla, Spillmann, & Watanabe, 1997), and the postulate of a perceptive field as the psychophysical analogue of the receptive field (Spillmann, Ransom-Hogg, & Oehler, 1987; Yu & Essock, 1996; Yazdanbakhsh & Gori, 2008). Reverse correlation has confirmed and extended the validity of the perceptive field concept by demonstrating that there are striking analogies between psychophysical measurements in human observers and single neurone responses in a number of tasks (Yu & Levi, 1997; Neri & Levi, 2006).

There is a *caveat*. According to Marr (1982) one cannot explain vision only at the level of neuronal correlates (the implementation level or hardware of vision). One also needs to explain it at the level of processes (the algorithmic level or software of vision) and at the level of adaptive function (the computational theory). In Marr's proposal, the three levels are complementary, in the sense that a real understanding of vision can emerge only when all three levels including their interrelations are understood.[2]

Phenomenology is not, in this way of thinking, a level of explanation. Rather, it provides the data for testing and thereby constrains the explanations because it defines what the end product of vision should be, what properties it should have, and how it should vary in certain contexts.

6. The correlative approach: how has it fared?

In retrospect it appears that the correlative approach has gained wide acceptance, benefiting enormously from questions raised by visual phenomenology (for review see Albright & Stoner, 2002). Who would have thought 50 years ago that there would be visual neurones responding as though they could mediate percepts, including Gestalt phenomena (Ehrenstein, Spillmann, & Sarris, 2003; Spillmann & Ehrenstein, 1996, 2004).

The finding that single-cell activity discriminates between simple disks and bars of different contrast, phase, wavelength, size, orientation, motion direction, and lateral disparity was a first important step (for review see Hubel, 1988). However, the breakthrough occurred when neurophysiologists advanced to higher perceptual processes, using novel and more complex stimuli such as had previously been described by phenomenologists.

For example, the finding by Baumgartner, von der Heydt, and Peterhans (1984) that neurones in area V2 of the rhesus monkey behave as though they could mediate the perception of illusory contours, firmly grounded visual perception in neurophysiology and prompted vision researchers to ask the question of "Where do visual signals become a perception?" (Baumgartner, 1990).

The concept of the *nonclassical receptive field*, i.e., surround modulation from beyond the classical receptive field (Baumgartner et al., 1984; Nelson & Frost, 1978; for review see Allman, Miezin, & McGuiness, 1985) pushed the door wide open for the study of contextual influences. Take a grey rectangle embedded in different surroundings: depending on the context it may be perceived as opaque, transparent, or in a different depth plane. What are the brain processes and their interactions that underlie such percepts?

To find the neuronal mechanisms that disambiguate such stimuli, researchers today employ contextual patterns, or even natural scenes. Some of these are similar to the patterns used by Gestalt psychologists, suggesting that Gestalt psychology within the context of today's neurophysiology is experiencing a renaissance (see the translation into English of Wolfgang Metzger's (1936) book *Gesetze des Sehens* [Laws of Seeing, 2006] seventy years after its first appearance). There is a difference: Computer-controlled displays and animations enable today's psychophysicists to study these phenomena not just qualitatively, but also quantitatively.

The list that follows gives an overview over a number of perceptual phenomena for which neurophysiological correlates have been described over the last 25 years, predominantly in the rhesus monkey (for review see Albright & Stoner, 2002). These findings suggest that those phenomena originate to a large extent, but not exclusively, from bottom-up mechanisms in early vision. Examples are ordered according to their presumed level of origin in visual areas V1–MT.

6.1. Area V1

6.1.1. Filling-in of the blind spot

The physiological blind spot is hardly ever seen, although it is represented in the brain (Tschermak, 1925). The optic disk, being devoid of photoreceptors, is fixed on the retina; the blind spot therefore represents a permanently stabilised image not unlike an afterimage. Such images are subject to local adaptation, i.e., they rapidly fade from view (Troxler effect) and become filled-in with the perceptual attributes of the surround. A plausible neuronal explanation for the filling-in of the blind spot is based on the finding that area V1-neurones in the contralateral representation of the optic disc respond to oriented bars presented across the blind spot, as if they were completed (Fiorani, Rosa, Gattass, & Rocha-Miranda, 1992). Most of these neurons have large binocular receptive fields that extend beyond the blind spot representation. Similar results were obtained with large homogenous surfaces, suggesting that visual information from the surround is entered into the blind spot area, filling-in the surface and rendering the blind spot invisible (Murakami, Komatsu, & Kinoshita, 1997; Komatsu, Kinoshita, & Murakami, 2000).

6.1.2. Filling-in of a lesion scotoma

As with the blind spot, a scotoma due to a retinal lesion is normally not noticed, even when projected against a white wall. For example, laser coagulation in diabetic patients produces numerous retinal scars, but rarely results in dark spots in perception. Spillmann and Werner (1996) proposed that a possible explanation for filling-in of a focal scotoma might arise from the fact that deafferented neurones in area V1 of the macaque become reactivated shortly after the lesion, suggesting input from outside the lesioned area. This stimulation is thought to occur by recruitment of collateral afferents and long-range horizontal interaction (Gilbert & Wiesel, 1992). The rearrangement increases the receptive field size (and location) of the silenced neurones, thereby enabling cells to fill in the lesioned area with featural information from the surround.

6.1.3. Filling-in of an artificial scotoma

Reorganization of receptive fields as just discussed for focal lesions may also account for the perceived filling-in of an artificial scotoma, i.e., an occluded or "empty" patch on a uniformly coloured surface (Pettet & Gilbert, 1992). Contrary to a lesion scotoma, strict fixation is required in order for an artificial scotoma to fade and become filled-in. This is because eye movements will counteract fading and keep brightness and colour of the enclosed surface area alive. Although a uniform surface supports no isomor-

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[2] Tse (2004): the brain is adaptable and "rewires" itself in response to stimulus requirement. Unlike computers, cerebral algorithms are implemented in the neural circuitry and are not run as programs on hardware.

phic cortical representation of its own (Friedman, Zhou, & von der Heydt, 2003), it is perceptually sustained by horizontal interactions from the edge signal, which is less prone to local adaptation. Once the edge signal is levelled due to fixation, the stimulus fills-in and rapidly fades from view (for review see Komatsu, 2006; Neumann, Yazdanbakhsh, & Mingolla, 2007; Paradiso et al., 2006).

6.1.4. Spatial integration of collinear contour segments

If we look around, we find that most objects in our world are given incompletely; to recognise them, the visual system must put together the pieces. A powerful mechanism that has evolved to perform this task is perceptual grouping across a gap. For example, collinear segments of a branch occluded by other branches, are spatially integrated in the interest of restoring the whole. Perceived grouping is likely achieved by neuronal connections that link up cells, which respond to iso-oriented, collinear contours (Schmidt, Goebel, Löwel, & Singer, 1997). This finding in the cat agrees with the behaviour of neurones in area V1 (V2) of the monkey that respond more strongly when a coaxial line is presented in the larger surround (e.g., Kapadia, Westheimer, Ito, & Gilbert, 1995; Nelson & Frost, 1985; Sillito, Grieve, Jones, Cudeiro, & Davis, 1995). The resulting facilitation appears to be related to the decrease in psychophysical threshold found with collinear flankers (e.g., Dresp & Bonnet, 1991), a finding that has been interpreted as a neuronal correlate of the *Gestalt factor of good continuation* (Polat & Sagi, 1994).

The same, or similar, neuronal mechanism may also underlie the perceptual grouping of coaxial Gabor patches embedded in a field of randomly oriented Gabor patches (Field, Hayes, & Hess, 1993; Kovacs & Julesz, 1993; Persike, 2008). When macaques were trained to detect a "hidden" Gabor figure, the spatio-temporal constraints required for contour integration were similar to those found in human vision (Mandon & Kreiter, 2005). A reasonable assumption is that in both species contour integration may be mediated via horizontal interactions in area V1 (Bauer & Heinze, 2002) or by feedback from extrastriate areas (Zipser, Lamme, & Schiller, 1996). On the other hand, the finding that objects embedded in fragmented stimulus patterns are recognised within less than 50 milliseconds makes an explanation by re-entrant signals unlikely and rather suggests a feed-forward mechanism (Kirchner & Thorpe, 2006).

6.1.5. Figure-ground segregation by orientation contrast

From texture experiments it is known that an area (e.g., a square) composed of iso-oriented slashes will pop out on a background texture that is oriented at right angles. In agreement with this percept, an individual line of given orientation elicits a stronger neuronal response in area V1 when surrounded by cross-oriented lines than by iso-oriented lines (Kastner, Nothdurft, & Pigarev, 1999; Knierim & van Essen, 1992; Sillito & Jones, 1996). Lamme (1995) has shown that the neuronal response to a figure defined by orientation contrast is similarly enhanced, even when the receptive field of the neurone is fully enclosed within the figural area, i.e., with no direct access to the stimulus surround (see also Zipser et al., 1996). This finding suggests that figure-ground segregation arises from long-range lateral interaction in early vision, possibly with feedback from higher cortical areas.

6.1.6. Amodal completion underneath an occluding surface

Most of our perception is stimulus-bound, yet there are exceptions. A stimulus is said to complete amodally when it appears to continue behind a gap, although the missing section is not actually seen. There are cells in area V1 of the monkey that respond to stimuli eliciting amodal completion in human observers, but fail to do so, when completion is absent. For example, responses suggestive of amodal completion across a *stereoscopically* presented gap were demonstrated in the monkey, when collinear line segments were positioned on opposite sides of the classical receptive field (Sugita, 1999). Characteristically, neurones responded only when the gap was presented in front of the line segments (i.e., consistent with occlusion), not behind.

6.1.7. Motion transparency

Motion transparency refers to the perception of a transparent surface elicited by motion, such as in plaids. Typically, each plane has a different motion direction and/or motion vector by which individual surfaces in a complex visual scene are perceptually segregated. Cells in area V1 were found to respond to their preferred direction of movement under conditions, when human observers reported motion transparency. This suggests that different subpopulations of neurones tuned to different motion directions represent the early stage for surface segmentation by motion transparency (Snowden, Treue, Erickson, & Andersen, 1991). In contrast, area MT cells appeared to be suppressed under similar conditions.

6.2. Area V2

6.2.1. Modal completion by illusory contours

Modal perception includes the perception of illusory contours that are perceptually present, although there is no correlate for them in the physical stimulus. A prime example of modal completion is the Kanizsa triangle, which is characterised by illusory borders bridging the gap between the corners (or pacmen). There is an equivalent in the realm of neurophysiology: Neurones in area V2 (and even V1) have been found to respond to the cues that induce illusory contours in human observers much in the same way as to real contours (Peterhans & von der Heydt, 1989, 1991; Redies, Crook, & Creutzfeldt, 1986; Von der Heydt, Peterhans, & Baumgartner, 1984). This is unexpected as the receptive field fell in-between the inducers with no access to the surround, and thus provides evidence for input from beyond the classical receptive field. The same neuronal mechanism has also been invoked to account for the crisp illusory line seen in Kanizsa's abutting gratings (Peterhans, von der Heydt, & Baumgartner, 1986; von der Heydt & Peterhans, 1989b). We have demonstrated that the psychophysical boundary conditions for the abutting grating illusion are consistent with the neurophysiological boundary conditions for this same illusion (Soriano, Spillmann, & Bach, 1996).

6.2.2. Border ownership (i.e., boundary assignment)

Rubin (1915/1921) was the first to state that the border belongs to the figure, not the ground. Consistent with this notion, neurones have been described in area V2 (and V1) of the monkey that respond more vigorously to a contrast edge attributable to the figure, rather than the ground (Baumann, van der Zwan, & Peterhans, 1997; Heider, Meskenaite, & Peterhans, 2000; Zhou, Friedman, & von der Heydt, 2000). This is illustrated by the parsing response of a single neurone in Fig. 2. Rubin also observed that a figure stands out relative to the ground, i.e., it looks closer to the observer. There is now evidence in area V2 neurones that depth information is encoded together with information for border ownership and surface representation (Bakin, Nakayama, & Gilbert, 2000; Qiu & von der Heydt, 2005). Furthermore, the same neurones that encode border ownership also respond more vigorously when attention is assigned to the figure (Qiu, Sugihara, & von der Heydt, 2007). It thus appears as though the very neurones that are responsible for figure-ground organisation are also involved in the selective enhancement of an object by attention, possibly by feedback from higher cortical levels.

6.2.3. Surface transparency and decomposition into multiple surfaces

Multiple surfaces stacked upon each other do not always result in perceptual occlusion. Given the right luminance hier-
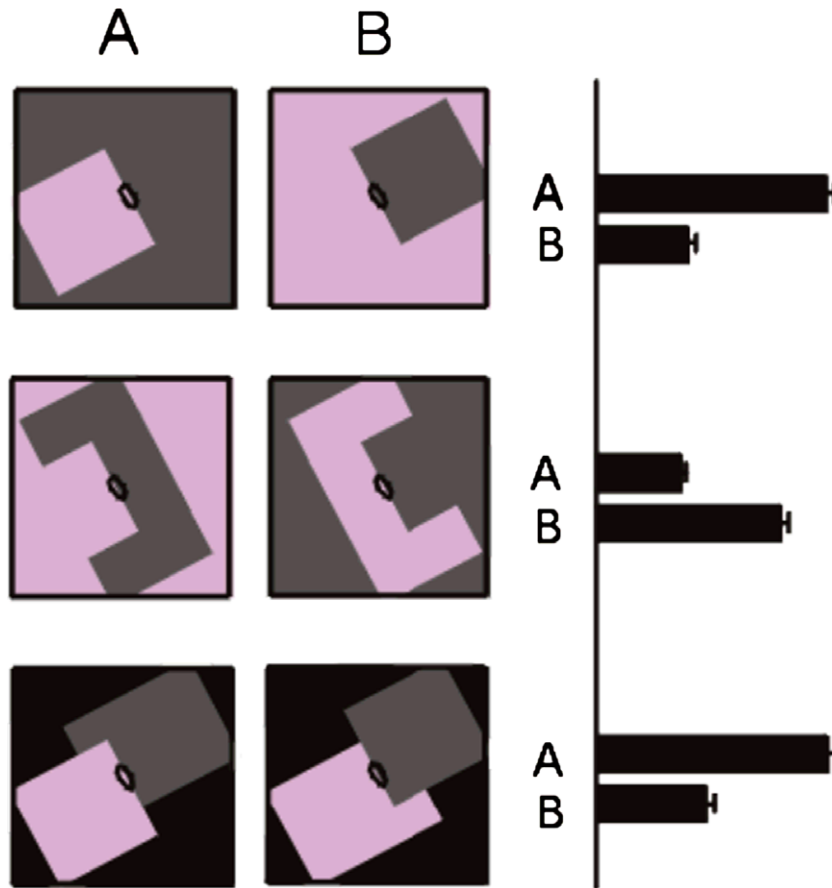
Fig. 2. Response of a neurone in area V2 tested with single squares, C-shaped stimuli and overlapping rectangles. The small ellipse represents the receptive field of a colour-selective cell with a preference for violet. The border between the two stimuli in columns A and B has the same contrast polarity (violet –> grey), but because stimuli have opposite figure-ground status, the border perceptually belongs to the violet square in the top and bottom panels (left) and to the violet C in the middle panel (right). As a rule, the neuronal response to the violet edge was far greater when it was owned by the figure than when it was part of the background (black columns on right). This asymmetry is interpreted in terms of border ownership (modified from Zhou, Friedman, & von der Heydt, 2000). (For interpretation of color mentioned in this figure the reader is referred to the web version of the article.)

archy, physically opaque surfaces are seen as transparent or semitransparent, allowing the bottom layers to be seen through the top (Da Pos, 1999; Metelli, 1974; for review see Gilchrist, 1994). Such stimuli are likely decomposed by neurones in Area V2 that assign border ownership consistent with the perception of a transparent overlay (Qiu & von der Heydt, 2007). The perceptual separation of a stimulus into an underlying surface and an overlaying layer is called *scission*.

6.2.4. Cyclopean perception

Depth from stereo cues (i.e., disparity) has been shown to arise from the correlation of pairs of random dot patterns none of which contains the image when viewed monocularly. Such patterns were originally developed by Julesz (1971) and termed cyclopean. Neuronal responses to stereoscopically fused half-images, such as those producing the percept of a diamond floating in depth, were demonstrated in area V2 of the behaving monkey (Von der Heydt, Zhou, & Friedman, 2000). Here, cells responded to stereoscopic edges by signalling their location, orientation, and depth polarity (near vs. far). This result supports the notion that figure-ground segregation by occlusion is primarily processed in area V2. It remains unknown how linear extrapolation can render the edges of a random dot stereogram perfectly straight, although straightness is not supported by the individual dots.

6.3. Area V3

6.3.1. Alignment in dotted contours

Whereas straight continuous lines are encoded in area V1, dotted lines are processed higher up. Neurones in area V3 (weaker in V2 and V1) respond to a group of collinearly arranged dots moving coherently on a uniform background much in the same way as to a continuous bar. Yet, they are extremely sensitive to misalignment as are we. The response breaks down, if only one dot is not in register. Results suggest that primate visual cortex detects and processes straight lines made up from sparse stimuli, and that this function evolves at a relatively early stage of visual processing (Peterhans, Heider, & Baumann, 2005).

6.3.2. Filling-in with dynamic texture

Surface completion by filling-in of a textural surface, as opposed to a uniformly bright or coloured surface, also occurs in area V3. This has been demonstrated in the monkey, by using a grey square ("hole") on a background of dynamic, vertical slashes. The receptive field of the neurone was placed entirely within the grey square, thus preventing any direct input from the surround. After an initial ON-response, the firing rate dropped to the baseline, then slowly increased again until the response matched that to a control stimulus (i.e., no hole). At this point the neurone was assumed to be unable to distinguish between the two conditions. This finding suggests that the missing information (dynamic texture) within

the hole had been fully recovered from the surround. The time course of the recovery (climbing response) was comparable to the time required for perceptual filling-in in human observers, suggesting that one is the correlate of the other (DeWeerd, Gattas, Desimone, & Ungerleider, 1995; for review see Spillmann & DeWeerd, 2003).

6.4. Area V4

6.4.1. Colour constancy

Among perceptual constancies, invariance of perceived colour under conditions of changing illumination is of great biological importance. It enables us to recognise objects irrespective of the wavelength spectra of the reflected light. However, colour constancy obtains only for broadband illumination of the entire scene; illumination of the object with narrowband light or in isolation dramatically changes its chromatic appearance. "Perceptual" neurones in area V4 of the monkey have been reported to respond to a coloured patch in a Mondrian pattern independently of the spectral illumination, so as to suggest colour constancy (Zeki, 1983). At lower levels (V1 and V2), no invariance was found between percept and neuronal response, when a disc of given colour (say red) surrounded by an annulus of different colour (say green) changed its appearance due to filling-in. Here, the neuronal response remained tied to the spectral properties of the stimulus ("red") despite the perceived hue shift (Von der Heydt, Friedman, & Zhou, 2003).

6.5. Area MT/MST

6.5.1. Shape by accretion/deletion

Motion links stimuli together as long as they move together. This also applies to form-from-motion defined by dynamic occlusion such as achieved by accretion and deletion (Shipley & Kellman, 1997). By progressively covering and uncovering the edges of an area, a global surface arises that is based on sequential changes of local motions integrated across space. Whereas an early study (Sary, Vogels, Kovacs, & Orban, 1995) reported cells in inferotemporal cortex that responded to kinetic boundaries, a later study described neurones that can account for dynamic shape perception in area MT (Stoner, Duncan, & Albright, 1998).

6.5.2. Grouping by coherent motion

Figure-ground segregation does not depend on surfaces. It also occurs with discrete stimuli in the absence of a cohesive surface. For example, when a group of individual dots moves coherently on a background of randomly moving dots, it assumes the status of a figure (Stürzel & Spillmann, 2004; Uttal, Spillmann, Stürzel, & Sekuler, 2000). This grouping may be mediated by neurones in area MT that respond to coherent motion and thereby account for the enormous power of the *Gestalt factor of common fate* as a segmentation factor. A dynamic visual acuity test based on form-from-motion (Wist, Ehrenstein, & Schrauf, 1998) is based on the same principle. The perceived figural segmentation in such patterns has been attributed to temporal coupling of spike chains via response synchronisation (Eckhorn, 1991; Gray, König, Engel, & Singer, 1989; Singer, 1989); and it has been interpreted in terms of Gestalt-like feature binding (Singer, 1989). In a remarkable experiment (Britten, Shadlen, Newsome, & Movshon, 1992) using trained rhesus monkeys, the sensitivity of individual MT cells to coherent motion was shown to be very similar to the monkeys' psychophysical sensitivity. This is evidence that the detection of motion is tied to the strength of the neuronal motion signal. Furthermore, in behavioural experiments monkeys were found to discriminate motion-defined shapes just as well as human observers, suggesting that both species rely on common neural mechanisms for this task (Unno, Kuno, Inoue, Nagasaka, & Mikami, 2003).

6.5.3. Apparent motion in motion quartets

Coherence of a different kind may be demonstrated in the bistable motion quartet (Ramachandran & Anstis, 1986). Here, either horizontal (zig-zag) or vertical (see-saw) apparent motion is seen between pairs of equispaced dots presented in successive frames. Using 16 such quartets arranged in an array, Schiller and Carvey (2006) demonstrated that contrary to the Gestalt factor of similarity the perceived direction of apparent motion is uniform regardless of differences in contrast, polarity, colour, or shape among pair members. This is consistent with the strong hysteresis effect found by Maloney, DalMartello, Sahm, and Spillmann (2005) in motion quartets. Significantly, Schiller and Carvey (2006) showed that uniformity of motion direction is disrupted by differences in size, proximity, or stereoscopic depth, provided these differences are large. These observations suggest that the midget (or parvocellular) system does not participate in generating the motion percept and suggests instead that the parasol (or magnocellular) system mediates the direction of apparent motion. The fact that all 16 quartets tend to move in unison points towards cells with large receptive fields, presumably in areas MT and MST. The apparent rotation of spoked wagon wheels under stroboscopic illumination, e.g., in old movies (Metzger, 1953), follows the same parametric rules. The motion quartet and the wagon wheel effect are beautiful examples of how brain mechanisms can be analysed by studying the perceptual effects arising from different stimulus parameters pitted against each other.

6.5.4. Motion in apertures

The direction of perceived motion normally is orthogonal to the orientation of a line stimulus. For example, a telegraph wire seen from a train window appears to move up and down, not along its own extent. Apertures can change this by forcing the motion direction to conform to the edges of the aperture (Wallach, 1935/1996). For example, in an L-shaped aperture, a diagonally oriented grating moving obliquely behind the aperture is seen to first move downward, then to the right. When neurones in MT were tested with such stimuli, they responded consistent with the *perceived* direction of motion. This suggests an influence of aperture orientation on neuronal direction selectivity (Duncan, Albright, & Stoner, 2000). These results are relevant for perceptually disambiguating extrinsic vs. intrinsic motion cues, i.e., ends of lines moving along the edge of the aperture vs. the lines themselves (Movshon, Adelson, Gizzi, & Newsome, 1985; Rust, Mante, Simoncelli, & Movshon, 2006; for review see Neumann et al., 2007).

6.5.5. Biological motion of point walkers

A fascinating experiment shows that a few small lights attached to the principal joints of a person will reveal that person's movements in an otherwise dark room. In fact, even an outline of the person can clearly be seen despite the sparse stimuli (Johansson, 1973). This is remarkable as the individual lights move in different directions and at different velocities and yet, they are integrated into a coherent motion (and shape) percept. Neurones have been reported in the anterior superior temporal polysensory area (STPa) of the monkey (Oram & Perrett, 1994) that discriminate a person from a jumble; they also signal, which way the sparsely represented persons, say two dancers, are facing and walking.

6.6. Functional brain architecture

The aforementioned results are summarized in Table 1 and suggest that in monkey visual cortex, occlusion cues for filling-in and completion, including the perception of cyclopean depth, are predominantly processed in areas V1 and V2, whereas mechanisms for grouping and motion are found mostly in areas V3 and MT. Coloured stimuli are processed in area V4. This list is destined to grow

Table 1
Visual percepts and their presumed level of neuronal origin.

Area V1
Filling-in of the blind spot
Filling-in of a lesion scotoma
Filling-in of an artificial scotoma
Spatial integration of collinear contour segments
Figure-ground segmentation by orientation contrast
Amodal completion underneath an occluding surface
Motion transparency

Area V2
Modal completion by illusory contours
Border ownership (boundary assignment)
Surface transparency/decomposition into multiple surfaces
Cyclopean perception

Area V3
Detection of alignment in dotted lines
Filling-in with dynamic texture

Area V4
Colour constancy

Area MT/MST
Shape by accretion/deletion
Grouping by coherent motion
Motion quartet: coherence disrupted
Motion direction in apertures
Biological motion in point walkers

as the boundaries of what is presently known keep advancing. Also, each of these effects probably is based on the interaction of many neurones, possibly connected across more than one cortical area and open to modulatory effects from higher levels. For these functions, feed-forward, feedback (re-entrant), and lateral (horizontal) connections are assumed in contextual (or second-order) receptive fields (Neumann et al., 2007).

The role played by reciprocal interactions between multiple cortical areas was revealed by (reversible) inactivation of area MT (Hupé et al., 1998). For example, cooling of area MT instantaneously affected the responses of V1, V2 and V3 neurones to patterns moving on a stationary background. This suggests that the segregation of such patterns into figure and ground may be influenced by signals fed back from MT to lower visual areas.

So far we have dealt with the phenomenological, psychophysical and neurophysiological aspects of visual perception. What about the topological aspects of vision in the cortex? Extending earlier work (Fischer, 1972; Tootell, Silverman, Switkes, & DeValois, 1982), Schwartz has arrived at accurate predictions of retinal projection onto the visual cortex. Fig. 3 illustrates the topographic representation of a circle, square, and triangle in area V1, demonstrating that retinal patterns projected onto the cerebral surface are visuotopic (or retinotopic), not isomorphic, with the visual stimulus. That is, geometric shape is not preserved. On the other hand, what is spatially contiguous on the retina is also next to each other on the cerebral cortex. The cortical representations shown in Fig. 3 are estimates of what one would observe from presenting a (centrally fixated) circle, square or triangle to a human subject, and then reconstructing a flattened picture of cortical fMRI activation. Note, however, that good retinotopic representation exists only in early visual cortex (e.g., areas V1–V3); at higher levels receptive fields are too large for detailed retinotopy.

We now know that there are numerous areas in the brain dedicated, exclusively or predominantly, to vision. To date more than thirty such areas with more than 300 interconnections have been identified in the primate (Felleman & Van Essen, 1991; Van Essen, Anderson, & Felleman, 1992). The majority of these are reciprocal. The question arises, why do we have all those areas in the brain?

One possibility is that the rich and complex world around us requires that a complex problem be subdivided into a number of
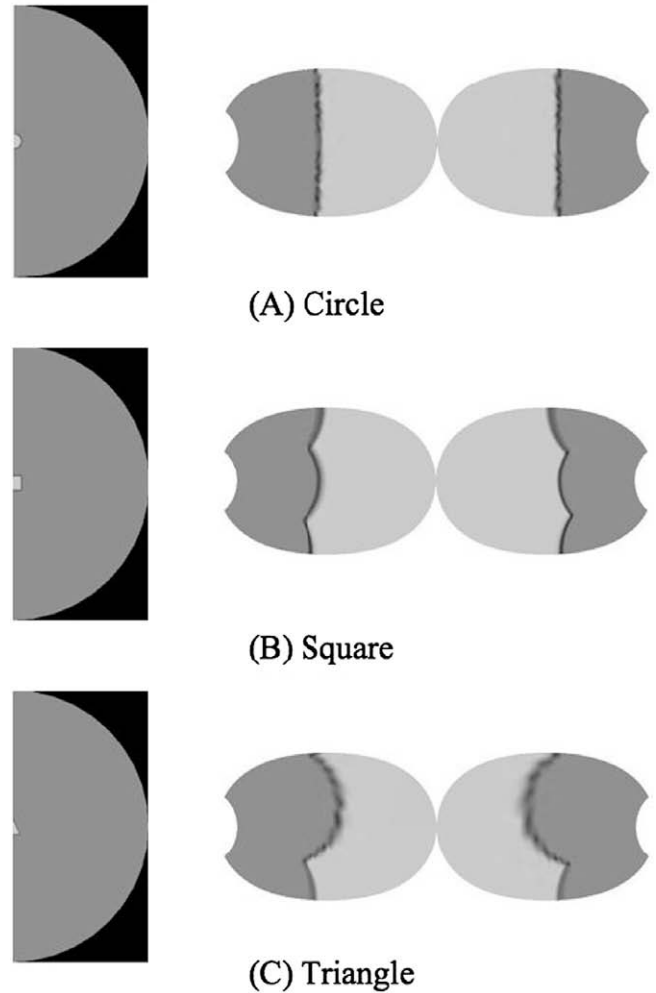
Fig. 3. Cortical representation of simple geometric patterns in area V1 of the human brain. In the left column are shown the hemi-retinal projections of a circle, square and triangle of size 12° (from top to bottom). The full visual field size is 120°, and only the right hemi-retina is shown. The oval-shaped figures next to it (on the right) show the corresponding cortical "images", using parameters estimated from human visuotopic mapping experiments (Hinds et al., 2008; Polimeni, Balasubramanian, & Schwartz, 2006). Both cortical hemispheres are shown: left hemisphere (right visual hemifield) is on the left and right hemisphere (left visual hemifield) on the right. The far periphery is oriented to the outside of the figures, and the foveal representation is oriented towards the centre. The light grey areas represent the interior of each pattern, the dark lines depict the edges (courtesy of Prof. Eric Schwartz).

smaller and simpler individual problems. These problems are then allocated to a distributed hierarchy of specialised areas for visual processing. Multiple maps have the advantage that cells subserving the same or similar functions (i.e., stimulus attributes) are clustered together in the interest of close connectivity and minimised wiring in intracortical circuits. This proximity then implies that segregation of features becomes more specific at successively higher stages of the visual system, whilst information on retinal position becomes less specific (Barlow, 1986; Chklovskii & Koulakov, 2004; Van Essen et al., 1992).

7. The need for neurophysiological correlations

The above examples (subchapters 6.1–6.6) bring physiological knowledge to phenomenological experience. When Liebmann, (1927/1996) made her observations on equiluminance, nothing was known about the neural pathway (or stream) carrying infor-

mation on colour to the brain (Livingstone & Hubel, 1987, 1988). Similarly, when Metzger published his *Gesetze des Sehens* (1936/2006), feature detectors in the visual system had not been discovered. Yet, these and other observations enable neuroscientists today to assign perceptual significance and meaning to the documented neuronal processes.

To be sure, phenomena can stand on their own, regardless of whether or not they are understood at the neuronal level. They do not become invalid, no matter how old they are and how often one looks at them. But in order to become research tools they need to be explained (Spillmann, 1994; Eysel, 2003; Troncoso, Macknik, & Martinez-Conde, 2005). Koffka's (1935) question 'Why do things look as they do?' (see also Epstein, 1994) cannot be answered without the help of neuronal mechanisms.

The different theoretical concepts may best be demonstrated by the long and passionate discussion surrounding the Kanizsa triangle (Spillmann & Dresp, 1995). Kanizsa (1955) argued that what the mind did was to complete the gaps between the inducers. The tendency to perceptually close the gaps between the inducers (according to the *Gestalt factor of closure*) was assumed to generate an apparent occluding surface. Others (e.g., Gregory, 1972) attributed the subjective contours to the visual system positing – on the basis of global pattern cues – the existence of a triangle that partially occludes the stimulus pattern (top-down).

In contrast to these cognitive accounts, neurophysiologists (Baumgartner et al., 1984; Redies et al., 1986; Peterhans & von der Heydt, 1989), seeking a neuronal correlate for the illusory completion of discontinuous lines, attributed the same contours to the activity of neurones in area V2 (and V1) (bottom-up).

The results by Baumgartner and colleagues on the Kanizsa triangle triggered an unparalleled research into the neurobiology of visual perception and helped to bridge the gap between psychophysics and neurophysiology. Meanwhile the evidence for a neuronal mechanism that elicits perception of the illusory contours in the Kanizsa triangle has been generally accepted, not the least because behavioural responses to Kanizsa type figures have been demonstrated even in birds, fishes, and insects (Nieder & Wagner, 1999; Wyzisk & Neumeyer, 2007), for which a cognitive account would not be appropriate.

What is the neurocomputational view of this? In terms of Marr's theory (1982), the neural correlate of the illusory contours constitutes the implementation level. This is an important part of the explanation, but not the only one. At the level of adaptive function, one wants to understand why it is useful for an organism to have perceptual mechanisms that make up illusory shapes. The reason is that visual information under natural conditions often is incomplete due to partial occlusion of the stimulus pattern, or even to the physiological blind spot. Thus, a mechanism that provides contour completion from retinal cues such as the 'pacmen' of the Kanizsa figures (*modal* completion) may just reflect the visual system's adaptation to incompleteness occurring in the environment. In evolutionary terms, it may even be thought of as a mechanism that evolved to counteract biological camouflage, e.g., arbitrary disruption of contours (Spillmann & Dresp, 1995). At the level of processes, finally, one would want to explain what exactly the brain is doing to generate the illusory triangle.

What is the role of phenomenology in all of this? It depends on what one counts as an explanation. But clearly, there are many aspects of the "why" and "how" of illusory figures that would never be captured by a strictly phenomenological description. On the other hand, a phenomenological description will constrain explanations at the different levels in important ways. For instance, it is well known that the phenomenology of the Kanizsa triangle not only includes the appearance of illusory contours, but also implies that the illusory shape defined by these contours takes on a
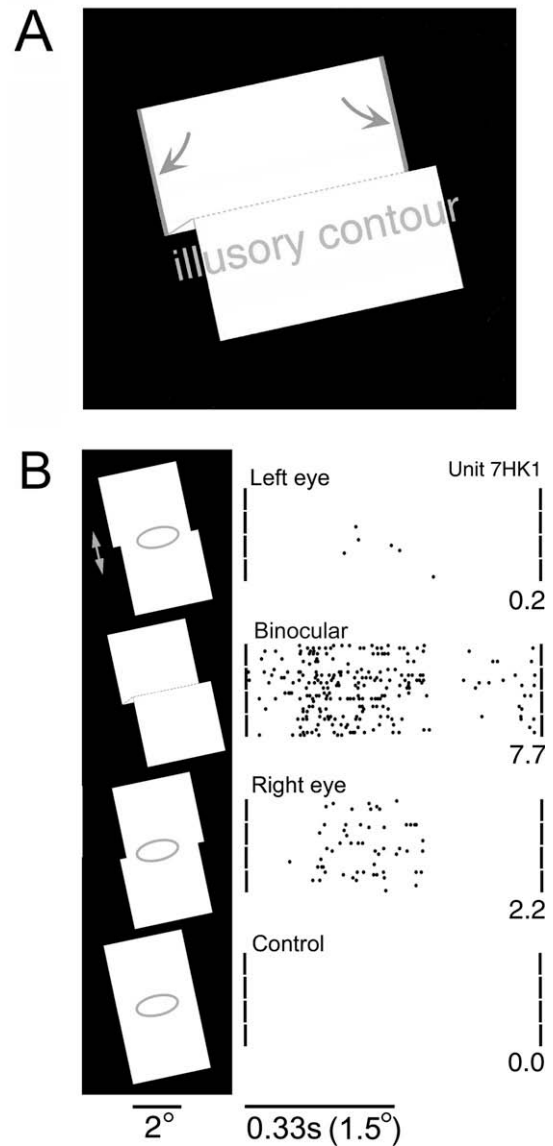
Fig. 4. Neurone response in area V2 of the monkey to a stimulus, eliciting an illusory step in depth. (A) Stimulus, if presented stereoscopically with a slight disparity, elicits the percept of an illusory contour and a step in depth between the two rectangles. (B) Neuronal response to a stimulus as shown in A. The ellipse denotes the response field of the neurone as measured with a light bar; note that both stereo cues at the left and right edge are located outside the response field. In the stimulus labelled "binocular," the upper rectangle is presented with an uncrossed disparity of 30′ and the lower rectangle with zero disparity. In the control stimulus both rectangles have zero disparity. Dot displays represent action potentials; responses recorded during the forward sweep of stimulus movement are shown in the left half, those recorded during the backward sweep in the right half. Note that the binocular presentation of the stimulus elicited a much stronger response than either of the two monocular presentations ("left and right eye", respectively), suggesting that the neurone processes disparity cues that give rise to depth stratification and illusory contour formation in perception (from Heider et al., 2002).

certain surface quality (i.e., brightness enhancement), and depth stratification.

The current neurophysiological explanation does not account for all three of these aspects, although the responses of a V2 neurone to a stimulus, eliciting the perception of an illusory stereostep in depth, suggest that illusory contours and depth stratification arise at the same level of visual processing (Heider, Spillmann, & Peterhans, 2002). This is shown in Fig. 4 and demonstrates that

the neuronal response to the binocular (3D) stimulus is stronger than to each of the two monocular stimuli.

8. Phenomenology and neurophysiology are complementary

Despite the separation into two camps, the phenomenological and the neurophysiological approaches to visual perception are not mutually exclusive in the sense of a dichotomy; rather, they complement each other. They may actually represent the two endpoints of a continuum. Needless to say, when the different approaches deal with the same phenomenon, their results must be compatible. For example, if a proposed neural mechanism fails to generate illusory contours in response to a set of 'pacmen,' that explanation is likely flawed.

One should bear in mind, however, that the complexity of the brain with its large number of visual areas and myriads of neurones and neuronal connections may preclude neurophysiologists from obtaining a comprehensive set of recordings that are associated with a given visual percept. In other words, if a putative neural mechanism fails to generate a certain perceptual phenomenon, this does not mean that such a mechanism does not exist.

Regardless of these limitations, phenomena deserve to be studied in their own right as they represent the material on which psychophysics and neurophysiology depend. This is consistent with Purkinje's (1819) *dictum* that perceptual phenomena reveal physiological truths, and is compatible with the classic observations by Mach (1865) and Hering (1874/1964) on border contrast and area contrast.

To account for the contrast bands bearing his name, Mach predicted the existence of lateral connections in the retina (see Ratliff, 1965), an insight that was inherent in the percept, not the physical stimulus. Similarly, Hering's colour theory was inspired by phenomenological observations on the incompatibility between opponent colours. Modern neurophysiology has confirmed a yellow–blue antagonism where yellow is achieved by the summation of the long- and medium-wavelength channels (red and green). An additive combination was also concluded from spatial and temporal studies of blackness induction, demonstrating that blackness is mediated by neural mechanisms that combine the outputs of middle- and long-wave cones (Volbrecht, Werner, & Cicerone, 1990).

Phenomena waiting to be assigned to a neural substrate are:

- The watercolour effect, a subtle and uniform colouration of a large surface area enclosed by a chromatic double contour (Pinna, Brelstaff, & Spillmann, 2001; Pinna & Grossberg, 2005; Von der Heydt & Pierson, 2006; Werner, Pinna, & Spillmann, 2007).
- The tunnel effect, demonstrating extrapolation of visual motion of an object disappearing behind, and reappearing from, a barrier (Michotte, 1946/63; Ryf & Ehrenstein, 1998; Takahashi et al., 2008; Vicario & Kiritani, 1999).

Neurocomputational models for these and other effects are becoming increasingly available (Grossberg & Mingolla, 1985; Neumann et al., 2007; Todorovic, 1998).

9. Going beyond correlations: why is the brain organised the way it is?

In retrospect, neurophysiological correlates to explain perceptual phenomena are only one aspect of vision research; for today's neurophysiologists the emphasis rather is to understand why the brain is organised the way it is as revealed by anatomical, neurophysiological, and imaging studies. This research is full of unexpected findings (Schiller, 1997). A few examples:

9.1. Retinal ON and OFF-cells

In the late 1930s, Hartline (1938, 1940) discovered that there are ON, OFF, and ON–OFF retinal ganglion cells, a finding that led to a Nobel Prize. Why did these systems emerge in the course of evolution? The most plausible hypothesis is that objects in the visual scene, depending on their reflection properties, become visible by either a light increment or light decrement, thus exciting ON- or OFF-cells, respectively. Using intracellular recording in the retina, subsequent work, e.g., by Werblin and Dowling (1969) in the mudpuppy (a large salamander) established that all photoreceptors hyperpolarise to light and that the ON- and OFF-systems arise at the bipolar cell level by virtue of sign-inverting (ON) and sign-conserving (OFF) synapses (for the mammalian retina see Wässle & Boycott, 1991). By selectively blocking the ON-channel, using the neuro-transmitter APB, Schiller (1982) then showed that in the primate visual system, the ON- and OFF-pathways remain largely segregated from the retina to the striate cortex. Detection of light increments, but not decrements, was severely impaired by injection of APB into the eye (Schiller, Sandell, & Maunsell, 1986). The central idea that has emerged from this work is that the ON- and OFF-channels have evolved to provide excitatory signals for both light and dark stimuli, an idea first proposed by Ewald Hering in the nineteenth century and reinforced in the 1950s by Jung et al. (1952) and Baumgartner (1961). Clearly, this was an unexpected finding of major importance.

9.2. Centre-surround organisation of receptive fields

In the 1950s, a major discovery by Kuffler (1953) was that retinal ganglion cells have a centre-surround organisation. Why has such an organisation emerged in the course of phylogenetic development? Studies have shown that the inhibitory surround enables the visual system to enhance edge contrast, sharpen spatial frequency channels, and suppress noise in the interest of optimising spatial resolution. In addition, during dark adaptation lateral inhibition in the receptive field decreases, thereby maximising sensitivity at the cost of resolution (Barlow, Fitzhugh, & Kuffler, 1957). The fact that retinal ganglion cells arranged in centre-surround receptive fields can function as local difference detectors enables the visual system to process pattern information over a huge range of illumination levels without a large dynamic range (Werblin, 1973). The discovery of the centre-surround antagonism has had a major impact in visual neuroscience as it is found from retina to cortex, and not just in the visual system. Receptive fields have been studied in other sense modalities (e.g., cutaneous) and in numerous species from Limulus to primates. What a great and unexpected discovery!

9.3. Orientation specificity of cortical cells

In the 1960s, Hubel and Wiesel (1965) found that the majority of cells in the visual cortex are orientation-specific, another finding that led to a Nobel Prize. Orientation-specific cells are tightly spaced in systematically arranged columns, representing the entire spectrum of orientations. Why did this columnar architecture emerge in the course of brain development? The initial idea was that pattern perception is accomplished by breaking down the visual scene into oriented line segments and that discrimination could be enhanced by inhibition between neighbouring orientation detectors (Blakemore, Carpenter, & Georgeson, 1970; Kurtenbach & Magnussen, 1981). Alternatively, it was proposed that pattern perception is accomplished by virtue of Fourier analysis in the visual cortex (Campbell & Robson, 1968). The fact that selectivity to orientation is orderly mapped onto the cerebral cortex points towards an explanation in terms of close connectivity and minimised wir-

ing, although other alternatives are still being discussed (Horton & Adams, 2005).

9.4. X/Y-cells of the cat and magno/parvo-cells of the monkey

In the 1970s, it was discovered that there are two distinct classes of retinal ganglion cells, called X and Y in cats (Boycott & Wässle, 1974; Cleland, Levick, & Sanderson, 1973; Shapley & Perry, 1986), or midget and parasol cells in primates (Schiller, Logothetis, & Charles, 1990). The midget cells projecting to the parvocellular layers of the LGN have relatively small receptive fields and process fine detail, colour, as well as fine stereopsis. This pathway has a high spatial and low temporal resolution, and is fairly insensitive to contrast, but colour-selective. In comparison, the parasol cells projecting to the magnocellular layers of the LGN have relatively large receptive fields and process motion and flicker, as well as coarse stereoscopic depth. This pathway has a low spatial and high temporal resolution, and is highly sensitive to contrast, but largely colour-blind. The central new idea proposed is that the midget cells have evolved to extend the range of vision in the wavelength and spatial domains, whereas the parasol cells have evolved to extend the range of vision in the luminance and temporal domain (Schiller et al., 1990). The finding that disparate stimulus parameters are processed by creating two distinct systems that originate in the retina was clearly a major discovery.

9.5. The "where" and "what" pathways

In the 1980s, it was shown that in primates visual processing at the level of the striate and prestriate cortex is far from complete, but continues into the parietal and temporal lobes (Mishkin, Ungerleider, & Macko, 1983). Following Schneider's (1969) finding in the hamster of two visual subsystems, one for exploration and one for close examination, the regions showing this functional specialisation have been called the "where" and the "what" systems. Research has shown that the first subserves spatial localisation and direction of motion (dorsal route), whilst the second deals with colour and object recognition (ventral route). There is evidence that these two pathways receive their inputs predominantly from the magnocellular and parvocellular systems of the retina, LGN and visual cortex, respectively. The magnocellular system projects to the parietal lobe, whereas the parvocellular system projects to the infero-temporal lobe (Hubel & Livingstone, 1987; Livingstone & Hubel, 1987). These processing streams provide the bases for early and mid-vision by linking the anatomical, functional and perceptual attributes together. A beautiful set of discoveries.

9.6. Transformation from 2D to 3D

A continuing problem throughout vision research – and the arts – has been the question of how two-dimensional images on the retinal surface can result in the perception of depth. The perception of depth is of major importance for spatial navigation, pursuit of prey, and flight from predators. So, how do we recover depth? Several factors are involved: binocular cues such as disparity and vergence, and monocular cues, such as motion parallax, shading, perspective, and accommodation. Neurophysiologists have established that there are neurones in areas V1 and V2 of the visual brain that respond selectively to different lateral disparities, thereby giving rise to stereoscopic depth perception (Poggio & Fischer, 1977); and that there are neurones in area MT sensitive to differential motion velocity, presumably contributing to motion parallax (Nadler, Angelaki, & DeAngelis, 2008). A behavioural experiment showed that when disparity and shading cues were presented together, monkeys performed better than with either cue alone, as did humans (Zhang, Weiner, Slocum, & Schiller, 2007). This suggests an interaction between the various cues for the optimal utilisation of depth stimuli and offers a challenge to single-cell neurophysiologists for future study.

9.7. Foveation of targets by saccadic eye movements

Vision without eye movements is crippling as is easily realised when one immobilises the eye muscles with curare (von Holst & Mittelstaedt, 1950). The ability of guided eye movements to bring the centre of gaze (fovea) onto a peripheral target greatly enhances the operational range of visual awareness. What is the neuronal machinery that helps us fixate and perform saccades? In anatomical studies, it was established that the mammalian retina projects to the superior colliculus and the lateral geniculate nucleus of the thalamus, which in turn projects to the visual cortex. So the question came up what are the roles of the retino-thalamic-cortical system as opposed to the retino-collicular systems in vision? We now know that the superior colliculus together with the frontal eye fields is involved in the generation of accurate eye movements (i.e., foveation) by utilizing an error signal, or vector code, that specifies the difference between the present and intended eye positions (Schiller, True, & Conway, 1979). Saccadic eye movements are essential for scutinizing peripheral objects. Without them we would see motion and temporal changes, but we would not know what the objects are.

Discoveries of this kind are largely the outgrowth of efforts that have addressed the question of why the brain has a plethora of neuronal systems as revealed by anatomical, physiological and imaging studies. This research strategy has had great success and, by providing a functional and structural framework, adds immeasurably to a better understanding of the neurophysiological correlates described above (chapter 6).

10. Outlook

A fitting culmination to the work of the past generation on parallels between phenomenological observation and single neurone responses would be a general account of Gestalt psychology's best-known descriptive principles (e.g., proximity, closure, good continuation, symmetry, similarity, and common fate). The generality of these principles in many kinds of percepts suggests that the physiological mechanisms may be implemented in multiple visual areas.

These neurophysiological mechanisms may be more universal than what we have discussed so far, because now one is looking beyond percept-to-cell correlates to principles for organising cortical functions, such as self-organising processes in the interest of the simplest, most regular and balanced field (*Prägnanzprinzip*). From such regularity must come the universal principles long asserted by the Gestaltists and yet to emerge, in what we may call *neo-Gestalt neurobiology*.

This paper shows that phenomenology and neurophysiology are not mutually exclusive, but complement each other. Phenomena in search of neurophysiological processes and neuronal mechanisms in search of phenomena are complementary strategies (Valberg & Lee, 1991). Although this relationship is mutual, it is not symmetrical. Whilst there are many phenomena that have spurred on the search for neuronal counterparts, there have been few neurophysiological findings that have led to new phenomena.

One example is the anthill effect (Nelson, 1974) that was inspired by known differences in the X- and Y-cell visual pathways. Here, two percepts were shown to alternate when looking at an anthill: a percept of "motion everywhere", including velocity and directional information, with positional informa-

tion being poor (the ants seem regularly spaced); and a percept of high visual acuity and recognition of detail around the point of fixation. Nelson argued that X- and Y-cells and their corresponding pathways in the temporal and parietal cortex are so different in their spatio-temporal properties that they cannot support two percepts, a global and a focal one, at the same time. Conscious perception therefore must choose – and will alternate – between them.

Fechner (1860/1966) would have called the complementary relationship between neural correlates and phenomena "inner psychophysics" as opposed to the relation between retinal stimuli and perceptions, i.e., "outer psychophysics." An account of visual perception requires a conceptual framework that describes, as well as explains, in neural terms, what we see, including illusions. Present-day physiological theories can explain only a fraction of our phenomenal experience. Future research will show more clearly the correlation between perceptual phenomena and neurophysiological processes. Any approach towards this goal is desirable and legitimate, but only a coherent integration of both, phenomenology and neuronal correlation, holds promise for the full picture.

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