

GESTALT ISSUES IN MODERN NEUROSCIENCE

ABSTRACT. We present select examples of how visual phenomena can serve as tools to uncover brain mechanisms. Specifically, *receptive field organization* is proposed as a Gestalt-like neural mechanism of perceptual organization. Appropriate phenomena, such as brightness and orientation contrast, subjective contours, filling-in, and aperture-viewed motion, allow for a quantitative comparison between receptive fields and their psychophysical counterparts, *perceptive* fields. Phenomenology might thus be extended from the study of perceptual qualities to their *transphenomenal substrates*, including memory functions. In conclusion, classic issues of Gestalt psychology can now be related to modern “Gestalt psychophysics” and neuroscience.

1. PHENOMENOLOGY AS A GUIDE TO BRAIN RESEARCH

The importance of phenomenology for perceptual research, emphasized by Gestalt psychology, has hardly seen a more creative proponent than the *spiritus rector* of the Trieste School of visual perception, Gaetano Kanizsa (1913–1993). By careful observation and artful variation of visual phenomena, Kanizsa revealed to us the puzzling and intriguing richness of perceptual experience. Phenomena are immediate (*direkt, unmittelbar*), reproducible, and undeniable facts of experience and hence a prime source of scientific investigation. Their description is - and should be - independent of the respective state of knowledge about sensory and brain functions as well as of the physical properties of the stimulus. Phenomenal description, however, is just the starting point of perceptual research and far from being self-sufficient. In order to understand the mechanisms of perception we need to know its *transphenomenal correlates* (see Köhler 1938), consisting of the physical stimulus and its sensory-neural processing (e.g., Baumgartner 1990, Barlow 1997).

Here we aim to show that phenomenology can be extended from the study of mere perceptual qualities to a powerful tool in search of brain functions. Kanizsa’s skeptical question “Können Sie das mit Einzelzellen erklären?” (Can you explain this [the illusory triangle] by single neurons?) (1982) asked on occasion of a talk in Zurich (see Spillmann 1999a, p. 1472) signifies the limitations of a “pure” phenomenological approach.



The subsequent success of the Zurich group (e.g., Baumgartner et al. 1984), in relating Gestalt phenomena to the activity of single neurons and neuronal networks in monkey and cat (Redies et al. 1986) came as a surprise not only to Kanizsa, but also to other psychologists at the time. Neurophysiologists grasped the significance of these findings more easily. Meanwhile, combining phenomenological observations with neurophysiological results to elucidate the brain correlates of perception has gained firm experimental support (e.g., Spillmann and Werner 1990, Barlow 1997, Nieder 2002, Spillmann and Ehrenstein 2003). In the following, we will present select examples of how classic issues of Gestalt psychology may be related to modern neuroscience and how visual phenomena can serve as tools to uncover brain mechanisms.

2. PURPOSE AND PROCESSING MODES OF PERCEPTION

A key assumption of Gestalt psychology is that percepts organize themselves according to the principle of greatest *Prägnanz*, i.e., in the simplest, most regular and balanced manner possible under the prevailing stimulus conditions. (“In allen Verläufen, welche überhaupt in zeitunabhängige Endzustände ausmünden, verschiebt sich die Ausbreitungsart in Richtung auf ein Minimum der Strukturenergie hin” (Köhler 1920, p. 250)). This tendency towards *Prägnanz* is supported by numerous examples (e.g., Wertheimer 1923, Metzger 1953). However, there are counterexamples showing that under certain circumstances the *Prägnanz* principle fails (Kanizsa 1994). Figure 1 shows an example taken from Pinna (1991). The empty space between the lines looks like a lemon-shaped surface (Figure 1a), despite the fact that the stimulus conditions favor the formation of a more regular pattern, i.e., a circle (Figure 1b). Conversely, in cases that obey the *Prägnanz* principle, there is no good explanation why we should see a stimulus pattern better than it is at the expense of veridicality. One may therefore ask, what purpose does the tendency towards *Prägnanz* serve?

A possible answer is optimization in the interest of robust transmission of information (Attneave 1959). Straight lines, continuous contours, symmetrical shapes are ubiquitous properties of natural objects. However, objects are rarely presented in their entirety. To make up for any stimulus occlusions or distortions, neuronal mechanisms may have evolved that strive to perceptually rectify crooked lines, fill in gaps, and complete patchy surfaces (akin to scotomata), thereby restoring the stimulus to its original state. What is known about such mechanisms that could potentially optimize information transmission?

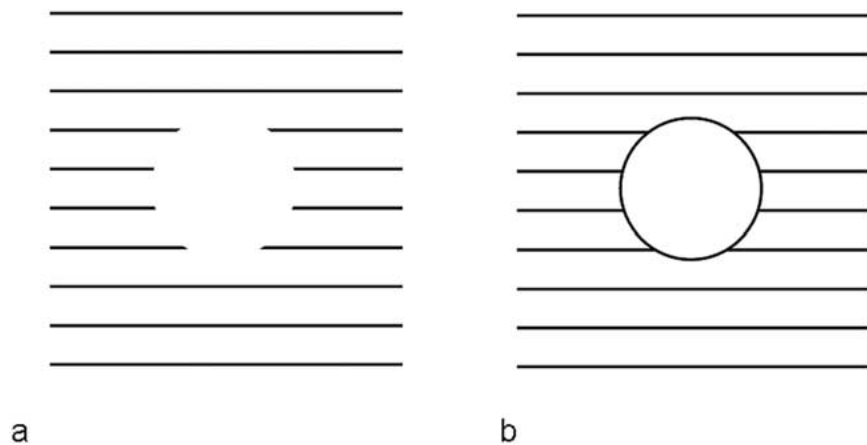
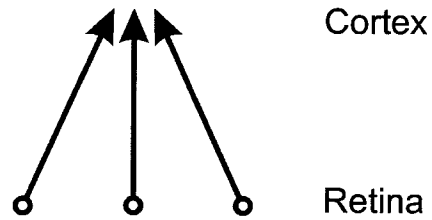


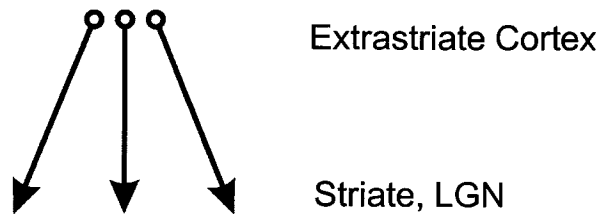
Figure 1. (a) The figure within the gap appears to be lemon-shaped, although the stimulus conditions allow for a perfect circle as in (b) where the subjective contour is replaced by a real contour (after Pinna 1991).

Neuroanatomical and neurophysiological studies have identified three main modes of information processing between the retina and the visual cortex (for a review see Spillmann 1999a). These are (a) *afferent*, bottom-up or feed-forward connections from the retina to the visual centers, (b) *efferent*, top-down or feedback connections from higher to lower cortical levels, and (c) *horizontal*, long-range or *lateral connections* within the same cortical layer (Figure 2). The first mode is implied if one understands Gestalt factors as *innate* conditions for the acquisition of visual experience about the world (Metzger 1953). The second mode reflects a modifying influence of the visual input by higher-order *cognitive* factors such as *Einstellung* (set) and selective attention. The third mode was anticipated with remarkable foresight by Max Wertheimer in 1912, when he attributed apparent motion to an *intracortical* short-circuit between two foci of excitation. Apparent motion occurs when two static lights are presented briefly in a proper sequence. Under these conditions one can perceive either pure motion without object displacement (phi motion) or, when the time interval between the two stimuli is slightly increased, a single moving light (optimal motion). In this case, perceived motion cannot be reduced to the two static stimulus events nor to the two single retinal processes elicited by them. To account for this nonadditive perceptual (Gestalt) quality, Wertheimer (1912, p. 247) assumed central processes, “physiological lateral interactions of a special kind that serve as the physiological correlate of the phi phenomena”. Today’s research has confirmed – and extended – this assumption about neuronal processing envisioned by the early Gestaltists.

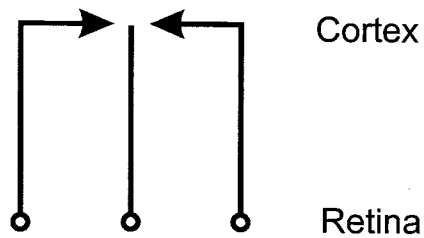
Three Types of Long-range Mechanisms



(a) Converging feed-forward connections



(b) Reentrant (feedback) connections



(c) Horizontal intrinsic connections

Figure 2. Modes of information processing within the visual system (schematic). (a) Converging connections from retina to cortex. (b) Re-entrant connections from higher to lower cortical and thalamic levels. (c) Cortico-cortical connections within the same layer.

3. RECEPTIVE FIELD AS A FUNCTIONAL MICRO-GESTALT

A basic notion worked out by Gestalt psychology (e.g., in studies of the *Ganzfeld* by Metzger, 1930, and of figure-ground segregation by Ehrenstein, 1930) is the need for sufficient contrast of the visual stimulus. Unless the contrast of a stimulus is above threshold (absolute or differential), Gestalt factors cannot act on it. In order for structural (Gestalt) laws to become effective, there must be something to work on (material, stuff). A figure will not emerge on a background when its contrast is too low (subliminal). Therefore, the first requirement for seeing is a *supra-threshold contrast* of the stimulus.

The neuronal mechanism that encodes physical contrast is the *receptive field organization*. The receptive field of a visual neuron is that area of the visual field (or its corresponding area on the retina) within which a change of luminance induces a change of the neuronal response. The receptive fields of retinal neurons are subdivided into a circular center and a concentric surround. The center and the surround are antagonistically organized, thus light falling onto the center activates the neuron, whereas light falling onto the surround inhibits it (*On-center* neuron). In the opposite type of receptive field all signs are reversed: Light in the center inhibits, whereas light in the surround activates the neuron (*Off-center* neuron). On-center neurons are assumed to mediate the sensation of “brighter”, off-center neurons that of “darker” (Jung 1973).

Similar receptive fields encode spectral or chromatic stimuli (see Valberg 2001, for a review). Neurons with *double-opponent* receptive fields have been found to mediate color contrast. Importantly, ‘blue-yellow’ receptive fields possess less center-surround antagonism than ‘red-green’ receptive fields. However, even for red and green strict isoluminance does not suffice to delineate a surface: a small step in luminance is needed (Liebmann 1927; West et al. 1996). Thus, Metzger’s (1953) notion of *Farbsprung als Grenze* (color discontinuity as a border) needs to be qualified in that it refers to discontinuity of achromatic rather than chromatic colors.

Further research has shown a considerable degree of functional specialization, e.g., cells in area V4 dedicated to color, cells in area V5 to motion (Zeki 1993). There is also evidence of multi-purpose cells (Schiller 1996), allowing for flexible, context-sensitive interaction within distributed neural networks. Thus, receptive field organization with its various forms of center-surround antagonism and selective spatio-temporal sampling is a basic mechanism that allows for non-additive, Gestalt-like integration of the stimulus input. In this sense, Spillmann and Ehrenstein (1996) have proposed the receptive field as a functional *micro-Gestalt*.

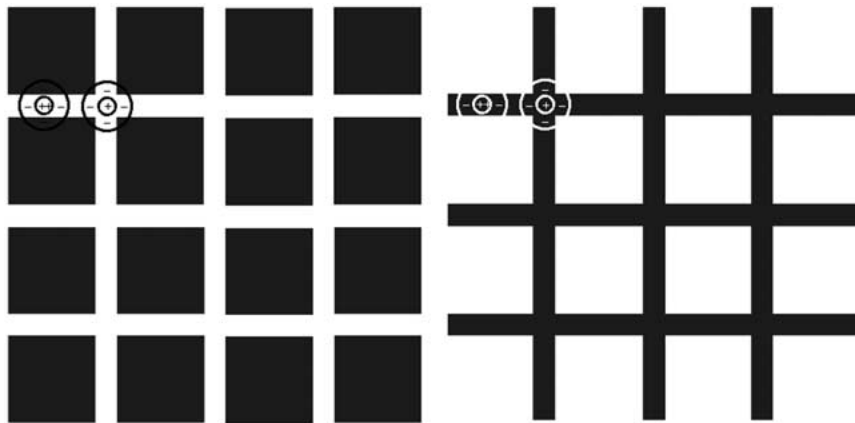


Figure 3. Hermann grid illusion. Dark (left) or bright (right) illusory blobs appear at the intersections, except when viewed foveally. If the width of the intersecting lines is sufficiently reduced or the viewing distance increased, the illusion also occurs in central vision. This suggests that foveal receptive fields are rather small.

3.1. Receptive and perceptive fields

A compelling and well-known phenomenon that may be explained in terms of concentric receptive fields is the Hermann grid illusion (Figure 3). Baumgartner (1960) first proposed that the dark illusory spots at the intersections of a white grid could be accounted for by the lesser activation of an *on-center* neuron at the intersection as compared to one bar only. Analogously, light illusory spots on a black grid may be attributed to the smaller amount of activation of an *off-center* neuron at the intersection as opposed to a single bar. The illusion is thought to be strongest when the width of the bar equals the diameter of a receptive field center at a given eccentricity. The Hermann grid illusion may therefore be used as a psychophysical probe to determine the size of human receptive field centers. Measurements performed at different eccentricities (Spillmann 1971, Spillmann et al. 1987) yielded values between 5' (in the fovea) and approx. 3° (in the outer periphery), thus reflecting an increase in field size similar to that found in primate physiology. The small size of receptive fields in the fovea explains why the Hermann grid illusion is typically not seen in the one intersection we are directly looking at.

In order to distinguish the neuronal receptive field from its psychophysical counterpart, Jung and Spillmann (1970) introduced the term *perceptive field*. Although psychophysical data represent the final stage of integration of the activity of numerous neurons, they are similar to those obtained with single cell recordings. Such similarities suggest that under certain conditions psychophysical correlates of neuronal mass function can be ascribed

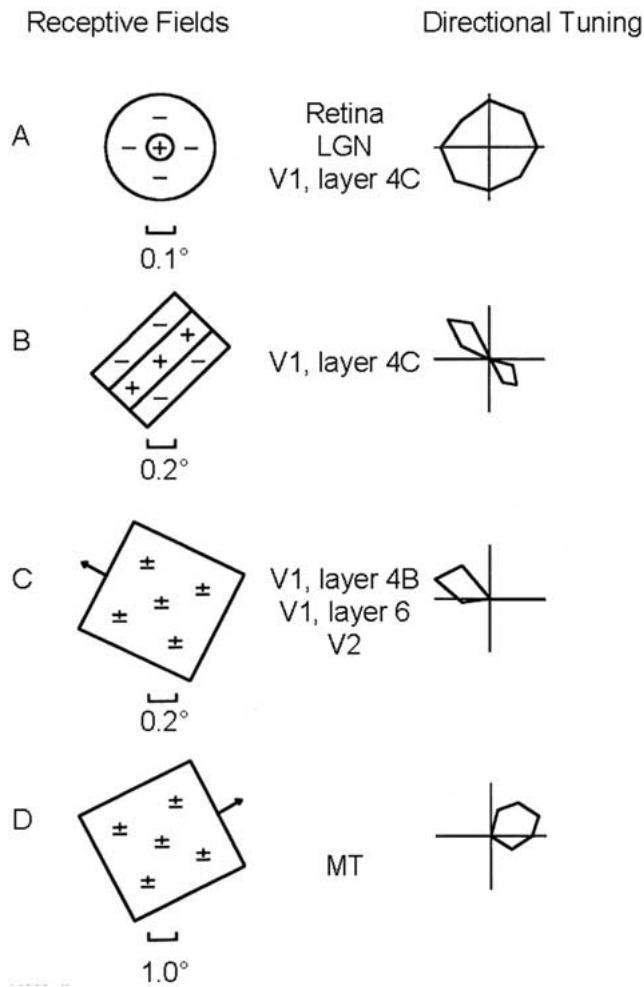


Figure 4. Receptive fields and tuning curves of neurons at various levels in the visual system (after Movshon 1990).

to the same principles that apply to single cells. Perceptive fields may thus be regarded as psychophysical equivalents of receptive fields with the conjecture that perceptual organization is largely determined by single-cell activity, organized within a hierarchy of receptive-fields (Ehrenstein 2001).

4. RECEPTIVE AND PERCEPTIVE FIELD ORGANIZATION

The Gestalt properties of receptive fields become even more apparent at higher levels of the visual system (Figure 4). A major change in receptive

field structure occurs at the cortical level. Whereas retinal and geniculate receptive fields have a circular center-surround structure, cortical receptive fields are elongated, as if formed by a number of overlapping, collinearly arranged geniculate receptive fields. Cortical receptive fields respond optimally to elongated stimuli, that is to bars and edges of a given orientation. They have therefore been labeled as *line or edge detectors*. However, receptive fields in the primary visual cortex are rather small (as compared to most objects in a visual scene) and therefore it is evident that perceiving the outline of a visual figure must involve many such neurons dynamically interacting with each other. There may be also cells that process the inner structure (*Binnenstruktur*) of visual figures, although the precise way in which a neuronal network processes intrafigural parts is still unknown. Creutzfeldt and Nothdurft (1978) demonstrated that the infrastructure of a figure such as a star, concentric circles, or a natural scene – and not just the outline – may be processed by single neurons in the primary cortex; this has been recently confirmed and extended by Martinez-Conde and Macknik (2001) for Vasarely patterns.

4.1. *Context neurons*

One may assume that Gestalt factors inherent in perceptual organization may be based on special *context neurons*, i.e., on cells that are sensitive to the context of the stimulus presented. Indeed, neurons have been found that respond differentially to *local* and *global* stimuli (e.g., Gilbert and Wiesel 1990; Kapadia et al. 2000; Wörgötter and Eysel 2000). For example, flanking segments located in the outer surround of a stimulus may modify the response to a small line segment of optimal orientation. While cross-orientation stimuli enhance the response, iso-orientation stimuli reduce it. When the surrounding segments are presented without a center stimulus, they are ineffective. This type of neuron therefore is likely to encode *orientation contrast* as a cue for figure-ground segregation.

Accordingly, Lamme (1995) showed that a hatched square will elicit different neuronal responses depending on whether it is placed on a cross- or iso-hatched background. In the former case the response is considerably higher than in the latter. Many such neurons together could thus set off the square relative to the ground by virtue of a higher firing rate at the edge. As the difference in orientation is reduced, the difference in neuronal excitation decreases, resulting in a smaller perceptual salience until the figure becomes embedded in the background and thus disappears from view. Analogous statements hold for perceptual *pop-out* due to differences in motion direction and speed (*motion contrast*).

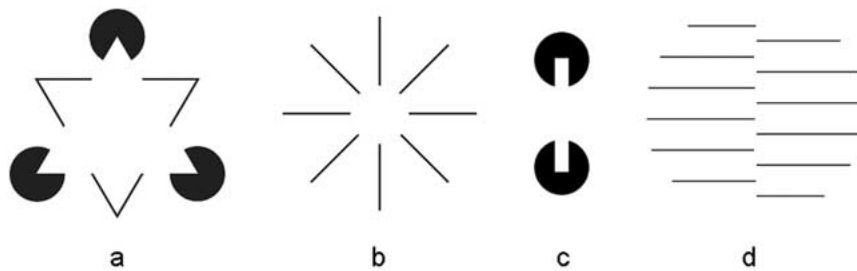


Figure 5. Four different stimulus patterns (a–d) eliciting the perception of illusory contours resulting in percepts of an illusory triangle, circle, bar, or vertical line, respectively.

Finally, there are neurons in monkey area V2 responding to *lateral disparity*, i.e., to the small differences between the two monocular images (von der Heydt et al. 2000). When binocularly fused such images produce stereo-depth. A stereo-edge has no physical correlate other than the disparity cues supporting it, and yet it can be seen as a crisp and very real change in depth between adjacent surfaces. Psychophysical measurements of the maximal distance across which a stereo-edge bridges a uniform interspace in human observers correlate well with cortical neuronal responses studied in monkey (Heider et al. 2002).

4.2. Edge-polarity neurons

Figures on a ground are privileged by being surrounded by a ‘unilateral’ border that separates them from the ground. In colloquial terms: The figure “owns” the border or else the border “belongs” to the figure, not to the ground. This qualifying feature was already known to Rubin (1915), who provided the first list of defining properties for a figure vis-à-vis the ground. It may now have found a neural correlate. Baumann et al. (1997) and Zhou et al. (2000) have reported edge polarity neurons in monkey areas V2 and V4 that respond to a light-dark step in one direction, but not in the other. Given the right direction of polarity this asymmetric response in conjunction with a closed contour could underlie “belongingness”. The responses of these neurons have been recently simulated by means of a grouping mechanism that uses occlusion cues (line ends, corners) to define figure-ground direction (Peterhans and Heitger 2001).

4.3. End-stopped units and neurons signaling subjective contours

Von der Heydt and Peterhans (1989) used the abutting grating illusion by Kanizsa, in which a thin contour appears to run in between the end points (terminators) of two horizontal, phase-shifted gratings opposing each other

(Figure 5d). In their model, two distinct mechanisms converge onto a common path. Oriented end-stopped units (in area V1 or V2), responding to the grating end-points, send their outputs to a higher-order neuron in area V2. This *contour neuron* samples the signals from V1 and then elicits a response that is similar to the response to a real vertical line (Figure 6). The boundary conditions found by recording from single cells in the monkey correlate closely with the boundary conditions for the perception of this illusion in human observers (Soriano et al. 1996).

The same kind of mechanism may explain the illusory contours in the Kanizsa triangle and the Ehrenstein circle (see Figure 5a, b). Baumgartner et al. (1984) showed for the first time that the response of a neuron in area V2 to an interrupted bar was qualitatively similar, although weaker, than the response of the same neuron to a continuous bar. This was surprising, as the receptive field of the neuron was never stimulated by the traversing stimulus. Even more surprising was the complete breakdown of the response when the top and bottom parts of the stimulus were “sealed off” by a thin line thereby destroying the percept of a subjective contour (Figure 6C). Baumgartner and coworkers therefore assumed that the neuron must have received input from areas outside the “classically defined receptive field” (*response field* to a bar or edge). The finding that the visual system includes neurons that respond to a stimulus giving rise to the perception of an illusory bar (or triangle, etc.), was the first evidence that the visual system is capable of *restoring* an incomplete stimulus.

Obviously, illusory contours were not given to us by nature to be enjoyed as curiosities. Rather, they are likely to be epi-phenomena of a mechanism that helps us to see partially occluded contours as belonging to the same object, such as the parts of a branch in a tree (Dresp 1997). The need for alignment in this task is crucial. Using a string of dots as a stimulus, Peterhans et al. (1986) found that a deviation of one of the dots by only 2 arc min from the theoretical curve completely offsets the response. This finding points towards *alignment detectors* governing the perception of illusory contours and good continuation (Peterhans and von der Heydt 1991, Kovacs and Julesz 1993).

4.4. *Signal propagation from the edge: Filling-in*

Computer simulations using different spatial filters demonstrate that much of the stimulus information is contained in the contour (Marr's, 1982, *primal sketch*). However, fortunately we not only see stick figures, but we also have access to uniform brightness, color, and texture that fill the enclosed surface area. How is this surface information represented in the visual cortex? From observations using strict visual fixation we know that

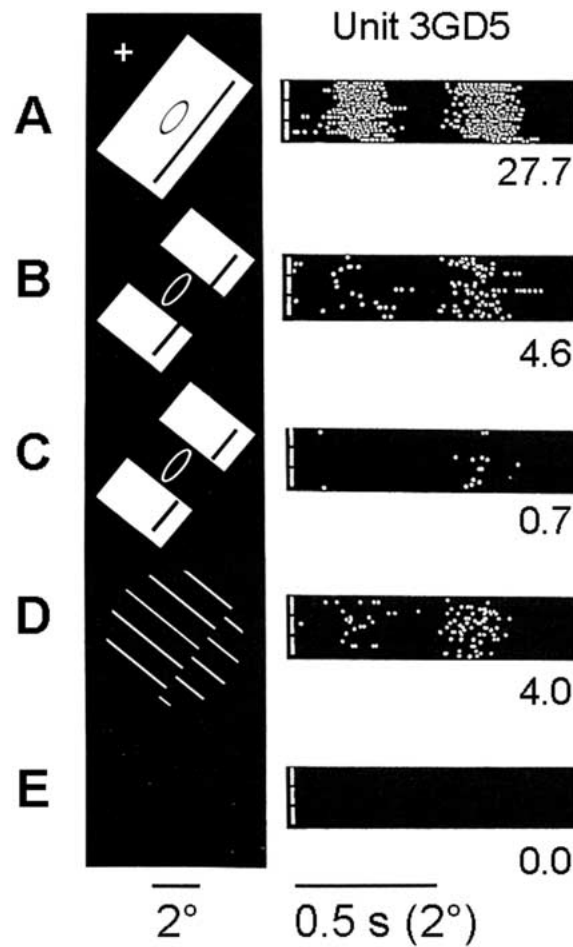


Figure 6. Responses of neurons in area V2 of the monkey. While the monkey is fixating a cross, the cell's response field (ellipse) is traversed by a bar moving back and forth (A), by a stimulus which elicits the percept of an illusory bar (B) or by an illusory contour produced by two abutting gratings (D). No stimulus is present in (E). The cell responds to the bar (A) as well as to the different illusory-contour stimuli (B, D), but not when stimulus (B) is slightly modified by adding a thin line to the top and bottom notches (C) which destroys the percept of an illusory bar (after Peterhans and von der Heydt 1991).

surfaces tend to become leveled relative to the ground and will even fade from view, due to local adaptation (*Troxler effect*). The main mechanism to overcome adaptation, and to sustain the perception of a surface over time is the continuous update of signals emanating from the edges. These signals are triggered by eye movements. On average, involuntary saccades will revive a percept four times a second thereby preventing its disappearance in the background (Gerrits et al. 1984). Two mechanisms have

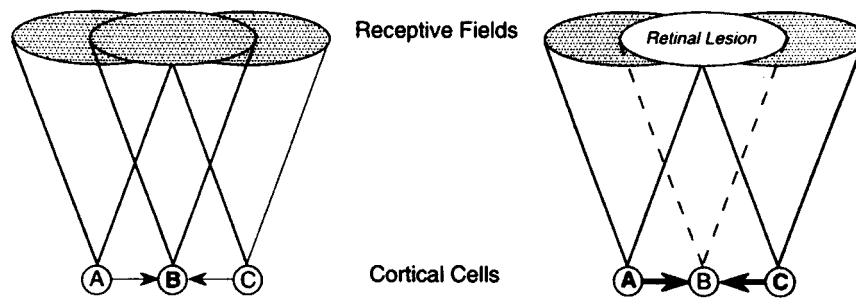


Figure 7. Schematic representation of three cortical neurons and their receptive fields (left side). If one of these fields (B) is destroyed by photo-coagulation of the retina (right side), the corresponding neuron falls silent. This deafferentation results in a blind area (scotoma) which, however, lasts only for a few minutes. When light falls onto the immediate surround, the neuron begins to “fire” again, suggesting neural reorganization and expansion of the receptive field (after Gilbert 1992).

been proposed (for a review see Spillmann and DeWeerd 2003): (i) Active filling-in by signal propagation from the edge; and (ii) generalization by a master neuron supplying the edge signal simultaneously to the entire enclosed area. Experimental evidence favors the first option (Paradiso and Nakayama 1991).

A similar mechanism appears to be responsible for the perceptual filling-in of a scotoma. Figure 7 (schematically) shows on the left three cortical neurons and their receptive fields. If one of these receptive fields (B) is destroyed by photocoagulation of the retina, the corresponding neuron falls silent because of deafferentation. The resulting percept is a hole in the visual field (scotoma). However, only a few minutes later, this same neuron will begin to “fire” again when light illuminates the immediate surround (Gilbert 1992). This effect may be explained by assuming that signals travelling along neighboring collaterals reach neuron B through horizontal axons from neurons A and C. These axons may normally be used for long-range propagation of brightness and color signals on extended surfaces (Spillmann and Werner 1996). When the primary input is missing, the connections from neighboring collaterals may become disinhibited and in this way provide neuron B with a much larger receptive field that includes the fields of neurons A and C. As a consequence, the scotoma is perceptually filled in with the properties of the surround and is no longer noticed.

4.5. *Component cells and pattern neurons: Local and global analysis of motion*

The perceived direction of moving contours depends on their spatial context, i.e., on the given shape of an “aperture” within which the moving

stimulus is viewed (Wallach 1935; Wuerger et al. 1996). Normally, the seen motion direction of a line with invisible end-points would be orthogonal to the line's orientation. In a window, however, the direction of motion typically is seen as parallel to the contour shape of the window. A striking example is the barber pole illusion, in which oblique lines, rotating horizontally around the vertical axis of a cylinder, appear to move upward (or downward) due to the vertical shape of the aperture. If the aperture is L-shaped, the moving lines change their direction from vertical to horizontal, when the lines reach the base of the L. The change in perceived motion direction is so compelling that it is hard to believe that the physical motion has not changed. This phenomenon refers to a general problem of motion analysis: How are the individual directions of local motion signals integrated so that they result in global motion events within a complex visual scene? The problem does not only reside on the phenomenological level. Neurophysiologically, the visual system faces the same problem in that limitations arise from the given shape and size of the receptive field of a single neuron (Adelson and Movshon 1982; van Wezel and Britten 2002).

A neurophysiological model to account for this problem was first proposed by Movshon et al. (1985). As in the model by Peterhans and von der Heydt (1989), two processing stages are assumed at different cortical levels: First-order direction-sensitive *component cells* in areas V1 and V2 and second-order *pattern cells* in area MT. These latter neurons have large receptive fields and receive direction-selective inputs from component cells of areas V1 and V2 that signal the local motions of individual contours. Pattern neurons in area MT integrate the information from local motion signals (e.g., from contours with different orientations) in a coherent global motion signal (see also Pack and Born 2001). An extension of Movshon's model to area MST, which borders on MT, has been recently proposed by Grossberg et al. (2001). They suggest that area MST provides a directional grouping network which further integrates the activity of transient short-range cells (V1) and long-range cells (MT). Thus, aperture-viewed motion has served and continues to inspire research and modeling of neuronal mechanisms in areas MT and MST that reveal integrative, Gestalt-like functions.

4.6. *Synchronized neural activity: Common fate*

So far we have linked visual phenomena to the properties of single neurons and their integration of spatial signals in specialized networks at various levels of the visual system. An additional mechanism that may achieve perceptual integration over extended areas of the visual field may be the

temporal binding of neuronal activity. Consider a figure composed of a number of dots on a randomly dotted background. As long as the figure remains static, it is embedded within the background dots and is thus invisible. However, as soon as it moves the figure pops out testifying to the enormous power of coherent motion. The Gestaltists called this principle of grouping the factor of *common fate*; it can tie together objects that are quite distant and different in form, size, or color. A trained monkey can discern behaviorally a group of 4–7 small dots moving coherently on a background of 100 random dots, and the same low signal-to-noise ratio is found for movement-sensitive neurons in visual area MT (Britten et al. 1992). Similar thresholds have been obtained psychophysically in human observers (Uttal et al. 2000). It has been proposed (e.g., Eckhorn et al. 1990; Singer and Gray 1995) that coherence is brought about by synchronization of oscillations in neurons “tagged” by a common feature (such as coherent motion). Dynamic grouping could thus result from temporarily binding of the activity of ever-new subsets of neurons with receptive fields in changing locations of the visual field.

5. GENERAL LINKING PROPOSITIONS: ISOMORPHISM

The present examples of linking visual experience to brain activity could be extended further to include also phenomena such as color spreading and transparency as well as aftereffects of color, size, shape, orientation, depth, and motion (see Spillmann and Ehrenstein 1996; 2003, for a review). Are there general rules of how visual phenomena are related to brain function?

An early attempt to arrive at a general *linking proposition* (Teller 1984) between perception and brain function was the Gestalt concept of *isomorphism* (Köhler 1920, p. 193). It postulates that every phenomenal (perceptual) state is linked to a structurally identical (isomorphic) neural process that occurs at a central level of the brain, the so-called *psychophysical level* (Köhler 1920, 1938). The search strategy underlying this analogy may be phrased as follows: At which level of the brain can we identify a pattern of neuronal activity that matches the percept more closely than the physical stimulus?

Alternatively, there is a second meaning to isomorphism, which focuses on the structural resemblance between the proximal stimulus (retinal image) and its representation on the cortical surface. Studies using radioactive tracers as well as functional magnetic resonance imaging (Tootell et al. 1998) have established a retinotopic, but not an isomorphic, representation of the stimulus in the cortex. That is, adjacent loci in the retinal image remain neighbors, but there is a complex logarithmic transformation between

retinal and cortical images, as well as anisotropies along the horizontal and vertical meridians (Wood and Schwartz 1999). The cortical magnification factor (M) demonstrates that the size of receptive fields is inversely related to their spatial extent in the visual cortex. Thus, when receptive fields of different eccentricity are M -scaled, they extend over the same space on the cortical surface (Wilson et al. 1990). For cortical area V1, M -scaling normalizes visual performances along a given meridian. There are, however, numerous other visual areas (e.g., V2 to V5, area MST) that lack the high magnification factor and retinotopic regularity of area V1. It would be tempting to understand the perceptual significance of the various spatial sampling properties of different visual cortical areas within the context of Gestalt psychology.

As yet, the phenomenon-centered Gestalt concept of isomorphism has received not much attention in neuroscience. One reason for this negligence can be seen in the failure of the early attempts by Köhler to find neural correlates of visual percepts. Meanwhile, thanks to the advanced methods of brain research and psychophysics (Ehrenstein and Ehrenstein 1999), the idea that perceptual phenomena are correlational counterparts of brain processes is gaining acceptance. Furthermore, neuroscientists have begun to address the brain correlates of consciousness (e.g., Crick and Koch 1998, Searle 2000, Engel and Singer 2001, Stoerig 2001). As a novel strategy, some groups have begun to look for neural correlates of percepts that lack a direct stimulus correlate (e.g., Macknik and Livingstone 1998, Spillmann 1999a, 2001).

6. FURTHER ISSUES OF GESTALT PSYCHOPHYSICS

So far we have dealt with phenomena that rely primarily on sensory functions. There are further, more complex, Gestalt phenomena that involve mnemonic functions and are determined by the respective *frame of reference* (*Bezugssystem*) or *transposition* of relational stimulus properties. These were important issues in the development of *Gestalt theory* (Wertheimer 1912, Köhler 1920). They are now increasingly subjected to detailed psychophysical investigation and quantitative modeling, an approach that we might call *Gestalt psychophysics*. The brain processes underlying many of the phenomena related to sensory and memory functions are still to be identified. They likely involve integrated neuronal networks rather than local cell properties. A promising approach is the comparative study of human and animal behavior and its development (e.g., Stebbins and Berkley 1990, Sarris 1994). It affords to bridge the gap between neurobiology

and psychophysics and also to specify the relevant parameters of future neurophysiological investigation.

6.1. *Frame of reference and relational psychophysics*

The concept of the *frame of reference* refers to the fact that identical stimuli can appear differently depending on the surround conditions. For instance, the same contour may appear either oblique or vertical depending on the shape of the frame (Wertheimer 1912). Frame-of-reference effects are closely related to the principles of *stimulus ratio* and *shifting level*, all of which are based on the general assumption that the effects of single stimuli are interrelated (Sarris 2003).

The *ratio principle* refers to the fact that a perceived quality is not locally determined, but is related to every other part of the visual field. For instance, the perception of surface lightness is based on the *ratio* between the light reflected from the figure to that reflected from its immediate surround (Wallach 1948; see also Gilchrist and Bonato 1995).

Likewise, the *shifting-level concept* refers to the dependence of a percept on the stimulus sequence (Koffka 1935). When an observer is repeatedly tested with either an ascending or descending stimulus series, whereby the physical values are gradually increased or diminished, systematic perceptual judgment “shifts” occur.

6.2. *Geometrical optical distortions*

Sarris and coworkers (cf. Sarris 1986) investigated two types of geometric-optical distortions, (a) distance or gap illusions, as the Delboeuf illusion; and (b) size or extent distortions, as the Baldwin illusion. The Ebbinghaus illusion belongs to the “mixed” type of geometric-optical distortions in that both the distance (D) and the surrounding context-size (B) may be systematically varied together with the focus stimulus (X) to be judged. This is illustrated in Figure 8 for varying contour size B (left) and distance D (right).

The systematic multi-factorial variation of the three major variables (B, D, X) gave experimental support to the different kinds of illusions, as predicted by Sarris (1986) in his *contour-distance* model. This line of research illustrates two research strategies: (a) A Gestalt-psychophysics approach based on a systematic multi-factorial design leading to new quantitative and qualitative results, (b) a type of research suggesting fruitful ideas as to the neurobiological mechanisms involved. More experiments are needed to better understand the underlying processes (see, however, Dücker 1966, Kanizsa et al. 1993, Nieder 2002).

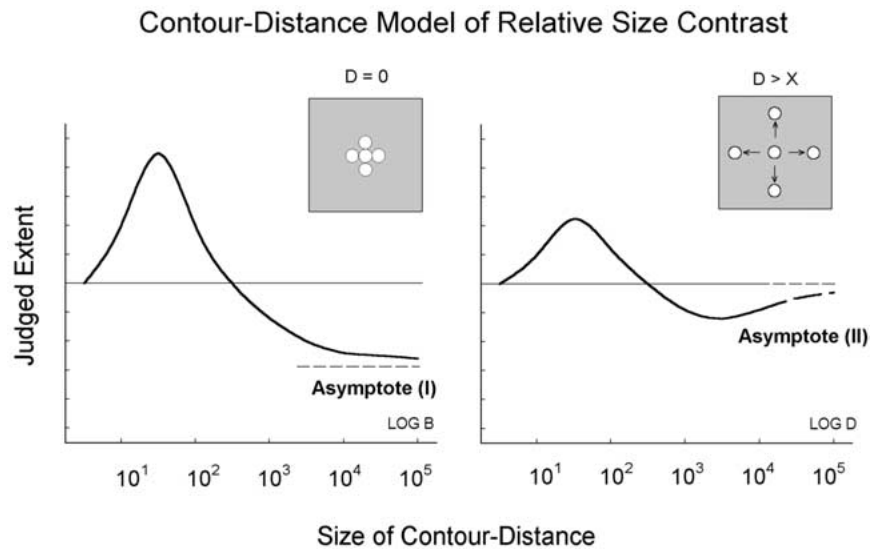


Figure 8. Predictions derived from a mathematical contour-distance model of relative size-contrast in the Ebbinghaus illusion (redrawn from Sarris 1986). The two predictive trends represent the over- vs. under-estimation (*assimilation* vs. *contrast*) in size of the focus circle (X). Left: contour-context prediction with variable background (B) and distance (D) at zero ($D = 0$); right: distance-context prediction with constant B and variable distance ($D > X$).

6.3. *Transposition*

The phenomenon of *transposition* refers to the fact that perception preserves the relations between stimuli, despite large changes in their absolute level. The study of transposition concerns the linkage of perceptual and mnemonic processes as already exemplified in Wolfgang Köhler's classic work on transposition in chickens, apes, and children (cf. Wertheimer 1959, Sarris 2001a, b). For example, a chicken is presented with two different sizes of squares, a smaller (A) and a larger one (B). After training to respond to B, it is tested over a period of time with a new pair of samples (B and C, where C is larger than B). Typically, the chicken will choose C over B during this test phase. This choice is based on relative rather than absolute stimulus properties, thus showing "*transposition*" which may be considered as a special case of the frame-of-reference effects (Sarris 2000, 2003).

6.4. *Comparative psychophysics of transposition*

Since animals are unlikely to react passively to a single stimulus dimension, a comparative psychophysics of transposition is needed (e.g., Lockhead 1992, Sarris 1994). In a series of *unidimensional* experiments

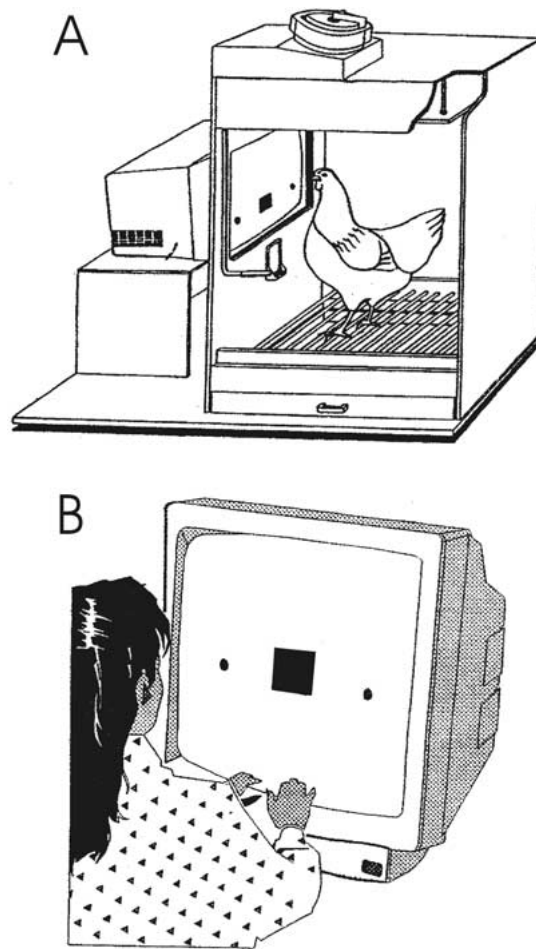


Figure 9. Touch-screen apparatus for the study of successive size-discrimination (training) and, thereafter, post-discrimination generalization of *context* effects (test phase). (A) Skinner box and touch screen, for the study of a chicken's behavior during training and testing of *context* effects; (B) touch screen, for human psychophysical settings (from Sarris 2003).

with different groups of chickens, a choice discrimination procedure, as employed previously in human subjects, was used followed by a generalization paradigm (Sarris 2003, Fig. 9).

Different-sized cubes served as a variable both during the training and test phases. During the training phase the animals learned to respond either to a "small" or a "large" box. They had to press the *right* key if the training cube was "small", and the *left* key if the cube was "large" (and *vice versa*). After reaching a 95% correct criterion, different subgroups of birds were tested with a variable context series of partly new boxes, either with

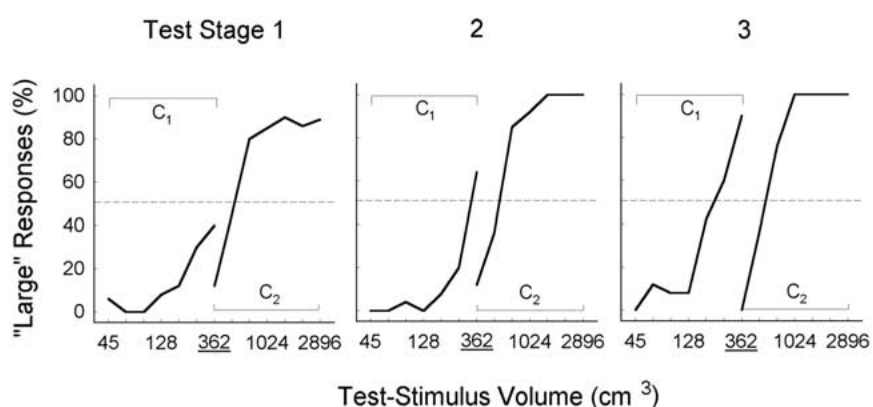


Figure 10. Development of context-dependent size-response behavior in chickens, during the post-discrimination test stages 1, 2, and 3. Note that the contextual responses develop only *gradually*, as predicted from a mathematical model (redrawn from Sarris 1994).

increasingly larger volumes or decreasingly smaller ones. In some other experiments the same chickens were trained and tested under all contextual conditions.

In all cases, the different test series provided the crucial role of contextual stimuli in that they were *asymmetrical* in comparison to the previously memorized training boxes (Figure 10). The chickens showed marked contextual effects during testing thus conforming to a large body of findings in human psychophysics. Note, however, that during the first test trials, chickens reacted to the stimuli as if they still belonged to the training-stimulus pair (*no context effect*). Only gradually, over the next series of test-trial stages, the birds “shifted” their response towards the new contextual test series. This frame-of-reference shift depended on the cube size of the contextual test boxes (*asymmetry effects*).

The unidimensional paradigm can be extended to a *multidimensional approach*. A simple example may illustrate the multidimensional problem of *relational psychophysics*. Everybody knows that jockeys are usually small and basketball players large. But at the same time we are able to judge an individual jockey as *large* and a basketball player as *small*. How do we develop such internal frame-of-reference systems? Are birds able to perform a two-dimensional psychophysical task such as this in a similar manner?

A four-stimulus-two-response discrimination paradigm was systematically employed with the stimulus material varying in two dimensions, i.e., training was performed with two different pairs of stimuli varying both in size and color. The results of this two-dimensional training and testing paradigm showed typical “relational” features in that one and the same

cube *size* elicited different responses depending on the *color* used. Apparently, chickens are able to respond to multidimensional objects according to rules which include the scaling of size and color variables (Sarris 2001b, 2003). Similar transposition effects occur already in the baby chick after 3–5 days of training and an additional 2–4 days of testing. Lawful generalization and transposition test data were obtained, with either size or color as the main psychophysical dimension (for details see Sarris 1998; Sarris et al. 1998, 2001).

6.5. *Transposition: A neural network account*

Can context-dependent effects of transpositional behavior, as found in humans and animals, be explained neurobiologically? In the absence of firm neurophysiological data, the following application and extension of a neural network model proposed by Johnson (1999) may be of interest. It assumes two process stages for the chick's brain-circuitry during the imprinting phase: A *subcortical* visual pathway and a *cortical* (forebrain) module in the intermediate, medial hyperstriatum ventral (IMHV) region.

Johnson (1999) simulated a range of perceptual learning phenomena associated with imprinting in the chick, especially within its *sensitive* or *critical* period. Such a neural network model might be useful not just to mimic the chick's most elementary behavior, but to also make *novel* predictions concerning "transposition" and "contextual" effects that occur during the post-discrimination phase of baby chicks. Although this model concerns a well-known neural circuitry in the chick, there is still insufficient knowledge of the more complex neurobiological processing involved during the first developmental perceptual stages. Johnson and co-workers have tried to also apply such modeling to the perceptual processes of human infants, for example, the Gestalt-like perception of the mother's face (cf. Johnson 1999). This concept might well serve to better understand the bio-psychological processes underlying the responses in *infant psychophysics* (see Teller 2000).

7. EPILOGUE

We have argued in favor of a wider scope of phenomenology, traditionally resident in philosophy and psychology, to enrich the perspectives of modern "Gestalt psychophysics" and brain research. There is an increasing dialogue between neurophysiological and psychophysical approaches so that with David Hubel, the renowned neurophysiologist, one may conclude that "gradually we are coming to understand each other's language and are

mastering each other's techniques. The field has become immeasurably richer" (Hubel 1995).

Combining phenomenal approaches with neurophysiology should not be confused with *neurophysiological reductionism*. As mentioned in the introduction, phenomena in their quality are independent of the knowledge of the brain processes underlying them. Percepts do not become deprived of anything if they are "consulted" to understand the functional processes that subserve them. Phenomena can rather serve to broaden and deepen the understanding of brain functions and give us a clue of why things look as they do (Spillmann 1999b, 2001).

The benefit is mutual: *Phenomena in search for mechanisms* represent a challenge for neurophysiologists and modelers since such mechanisms could not have been predicted from the physical stimulus. Vice versa, *mechanisms in search of phenomena* constitute a task for psychologists to look for percepts that may otherwise not have been uncovered. Both strategies complement each other in providing a better understanding of the visual brain so that Baumgartner's (1990) question: "Where do visual signals become a perception?" becomes meaningful.

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