Guest editorial: Colour in a larger perspective: the rebirth of Gestalt psychology

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Abstract. This overview takes the reader from the classical contrast and assimilation studies of the past to today's colour research, in a broad sense, with its renewed emphasis on the phenomenological qualities of visual perception. It shows how the shift in paradigm from local to global effects in single-unit recordings prompted a reappraisal of appearance in visual experiments, not just in colour, but in the perception of motion, texture, and depth as well. Gestalt ideas placed in the context of modern concepts are shown to inspire psychophysicists, neurophysiologists, and computational vision scientists alike. Feedforward, horizontal interactions, and feedback are discussed as potential neuronal mechanisms to account for phenomena such as uniform surfaces, filling-in, and grouping arising from processes beyond the classical receptive field. A look forward towards future developments in the field of figure–ground segregation (Gestalt formation) concludes the article.

During the past fifteen years, we have witnessed a neo-Gestalt approach emerging in the visual sciences that has deep historical roots in European psychology and at the same time unites several once separate fields and approaches. This and the previous special issue (Perception, 26 number 4, April 1997) on contextual colour effects may serve as a platform from which to consider this development and discuss vision and visual perception at large. It is an attempt combining many approaches (phenomenological, neurophysiological, computational) to identify possible underlying mechanisms. This interdisciplinary approach distinguishes present concepts of perceptual organisation from previous views (Wagemans and Kolinsky 1994) and offers a link between the past and the future for a better understanding of visual perception.

1 Colour and brightness on extended surfaces
The observation that an extended surface appears to change in brightness or hue in a way that depends on the luminance and colour of its surround goes back at least to Leonardo da Vinci and Goethe (Wade 1996). Chevreul (1839) was the first to study the phenomenon systematically when it was noticed that colours used in weaving tapestries looked different than expected. He demonstrated that this effect was not an artifact of manufacturing, but was produced perceptually by the coloured surround. About thirty years later, Ewald Hering (1878) published his famous treatise Zur Lehre vom Lichtsinn with a chapter dedicated to the phenomenon of ‘Flächenkontrast’ or surface contrast. Hess and Pretori (1894) measured these contrast effects psychophysically by matching the appearance of coloured papers surrounded by other colours with samples presented on a gray background. Jameson and Hurvich (1961) and Hurvich and Jameson (1966) elaborated on these findings in a remarkable series of studies and interpreted their results in terms of Hering's opponent-colour theory.

After a long period during which vision researchers and psychophysicists concentrated mainly on colour detection and discrimination, appearance has again been recognised as an important means for understanding colour perception (see the studies by Walraven 1973, 1976; Larimer et al 1975; and Werner et al 1984). A similar shift of emphasis has occurred in contemporary models of colour constancy (Maloney and Wandell 1986; McCann 1987; D'Zmura 1992) where colour descriptors had been used to account
for illumination invariance (Land 1983), but few attempts have been made to also model contextual effects on colour appearance.

This special issue is intended to encourage researchers to take an integrated approach towards contextual effects on colour appearance, encompassing visual percepts, neural mechanisms, and theoretical concepts. Since colour vision may be assumed to share mechanisms with other phenomena of lateral interaction, this editorial takes a broader view by including texture and motion perception as well. Although our understanding of the neural circuitry is limited, the phenomena under consideration are real and indisputable. To explain them we should use perceptual evidence in constraining our search for the underlying mechanisms. Surfaces enclosed by boundaries, rather than edge effects, have become the main focus of interest, and a cellular basis for these mechanisms will have to be sought in cortical visual areas rather than in interactive processes in the retina as originally proposed by Mach (1865). Such mechanisms would have to extend beyond the classical receptive field; and they might even have to allow for mutual interaction between any two points in the visual field, regardless of the distance between them (Hering 1878).

2 From local to global interaction
The shift in attention from contours and edges (in a broad sense) to uniform surfaces was stimulated by the neurophysiological study of Baumgartner et al (1984) on illusory contours in Kanizsa-type figures. These researchers recorded the response of 'contour neurons' in area V2 of the primate visual cortex to one of two types of stimuli: a continuous bar moving across the receptive field of the cell; and the top and bottom parts of this same bar (ie without the middle section) moving in the same manner, but outside the receptive field. In humans, this latter stimulus elicits perception of a bright illusory bar connecting across the gap. Baumgartner et al (1984) found that cells responded to the interrupted bar as if it had been a continuous bar, albeit more weakly. Apparently, information from regions beyond the classical receptive field contributed to the response. The idea of local versus global neural interaction had been proposed before (von Békésy 1968; Nelson and Frost 1978, 1985), but with the new evidence it took hold (for a review see Allman et al 1985). Since then the investigation of illusory contours and brightness enhancement effects has increased dramatically (see Spillmann and Dresp 1995; also Matthews and Welch, this issue), giving rise to computational (Grossberg 1984; Grossberg and Todorovic 1988; Heitger et al 1992), neurophysiological (Peterhans and von der Heydt 1989; Kapadia et al 1995), psychophysical (Gilbert 1992; Field et al 1993), and cognitive theorising (Rock 1987) on visual perception and brain science.

Based on these models, explanations have been proposed that invoke such concepts as early or low-level, intermediate or mid-level, and late or high-level vision. To account for contour integration, surface filling-in, and figure–ground segregation, a new vocabulary has emerged including such terms as edge assignment, border ownership, capture, belongingness, support ratio, relatability, and atmosphere. Curiously, some of these terms should sound familiar, as they are modern replicas of classic Gestalt nomenclature (cf Koffka 1935; Metzger 1953). Apparently, what had been assumed to be dead was only dormant, and is now being resurrected into the mainstream of today's perceptual psychology, often without awareness of the historical context from whence it came (see Spillmann and Ehrenstein 1996).

3 Rebirth of Gestalt psychology
The great Gestalt psychologists Wertheimer, Köhler, Koffka, Gelb, Duncker, Katz, Metzger, and Wallach would have rejoiced at today's increasing emphasis on the phenomena of figure–ground segregation, surface colour, and brightness. So too, would their Italian friends and colleagues Benussi, Musatti, Metelli, Kanizsa, and the Belgian psychologist Michotte, who for decades carried the banner of transparency, amodal completion, aperture
motion, kinetic depth effects, and phenomenal causality (ie a moving stimulus seemingly imparting movement to another). The renewed interest in these topics is amply reflected in Legrenzi and Bozzi's foreword to Gaetano Kanizsa's (1979) seminal book Organization in Vision (page VII): "At times it becomes necessary ... to seek the natural, primary source of the phenomena: the visual experience of ordinary seeing. Although the researchers who enjoy this way of exploring are not very numerous, in the past a great part of fruitful psychological research developed in this fashion."

Whereas the early Gestalt studies (summarised in Metzger 1953) were often conducted with only paper and pencil or the simple apparatus available at the time (eg Liebmann 1927; Wallach 1935), today's computer technology enables experimenters to display and control on their monitors complex stimuli that could not have been easily generated before. Distortions of the stimulus and optic flow fields produced by translation, rotation, contraction, and expansion are being used to study shape-from-motion, object motion, and self-motion in space (Anstis 1986; Tanaka and Saito 1989; Ramachandran 1992; Lappe et al 1996; Duffy and Wurtz 1997; Goda and Ejima, this issue). Ambiguous stimuli are generated for the study of aperture motion and plaid motion (Adelson and Movshon 1982; Stoner et al 1990). Similarly, kinetic random-dot fields are produced to investigate motion transparency and stratification, ie two populations of dots with different motion vectors are perceptually grouped into two transparent surfaces separated in depth (van Doorn and Koenderink 1982; Snowden et al 1991; Qian and Andersen 1994; Watanabe 1997). Depth segregation in a way is comparable to colour transparency. To accomplish scission (Metelli 1974) and thereby solve the problem of intermingling, the visual system uses the Gestalt factors of similarity and common fate.

No one yet knows precisely how the nervous system segregates such perceptual surfaces in neural space. However, the answers are likely to be the same for surfaces bounded by a luminance or reflectance edge (brightness, colour), or an edge defined by disparity (depth), motion contrast (shearing), orientation contrast (corners, slant), and texture contrast (Nothdurft 1993; Sary et al 1995; Bach and Meigen 1997; Schiller 1996; Zipser et al 1996). By analysing the effect of any of these borders on the neuronal response to a uniform area (reversed mapping), the neurophysiological study of figure - ground relationships in the primary visual cortex has now become possible (Lamme 1995) — with most exciting results.

In addition to the above attributes, Kennedy (1987) distinguishes between the following major dimensions of surface variation: (i) geometry of surfaces — coplanarity, corners, and occluding edges; (ii) opacity and transparency of surfaces; (iii) reflectance of surfaces — shiny or matte; (iv) illumination on surfaces — shadows and highlights. The role of accretion and deletion of elements by dynamic occlusion first explored by Michotte (1946) and Kaplan (1969) is yet another topic that is being actively studied in connection with the perception of subjective contours, neon colour, transparency, and shape (Shipley and Kellman 1994; Cunningham et al, in press; Cicerone and Hoffman, this issue; Miyahara and Cicerone, this issue.) Often, accretion and deletion of elements occurring across time use the same geometry that governs binocular disparity of elements across space, and the two are therefore closely related stimuli, highly effective for surface-boundary and depth perception.

We are far from being able to account for these surface qualities in terms of neuronal processes. However, three principal mechanisms are being discussed to explain how extended areas are segregated from their surrounds: feedforward (retino-geniculo-cortical) projections, horizontal (cortico-cortical) interactions, and feedback (re-entrant) projections (Spillmann and Werner 1996). All three mechanisms include central processing at various levels of the visual pathway and may occur together. How such mechanisms compute large-scale surface properties such as brightness, colour, and depth from local features — indeed, how they construct the surfaces themselves from complex natural scenes — is one of the most urgent questions in today's visual science.
4 Uniform surfaces produced by converging feedforward

Neurophysiological approaches to surface uniformity and filling-in based on hierarchical convergence (Hubel and Wiesel 1962) are challenged by the lack of specific models of large-scale neuronal processing. From the point of an isomorphic representation, end-stopping as a mechanism to account for illusory contour formation (Baumgartner et al. 1984; Baumann et al 1997) fails to explain how surface brightness and colour can extend far beyond the localised range of that operation. The computational approach by Grossberg and Mingolla (1985a, 1985b) and Gove et al (1995) on the complementarity of form (BCS) and colour appearance (FCS) offers new insights into potential neural solutions, as it proposes for both subsystems context-sensitive mechanisms that extend far beyond the spatial range of a simple filtering operation. Yet, their proposal that a boundary-gated 'diffusion' can occur within bounded regions remains hypothetical as long as there is little or no clear physiological evidence for diffuse propagation. On the other hand, neurophysiological studies on cells in the primate visual area V4 having receptive fields with extended chromatic surrounds (Schein and Desimone 1990) and on contextual neurons responding to a patch in a Mondrian pattern as though they could 'perceive' the colour, irrespective of its wavelength (Zeki 1983), suggest possible mechanisms for colour contrast and constancy. Recent work by Kitano and colleagues (1994, 1995) on long-range propagation of stimulus-locked field potentials in the striate cortex of the cat may also be relevant.

In a psychophysical experiment, Paradiso and Nakayama (1991) studied filling-in as a function of time. They concluded that filling-in is a gradual process, flowing from the edge of a surface to the enclosed region, and that it can be obstructed by boundaries, just as Grossberg and Todorovic (1988) predicted. (For a model of the time course see Arrington 1994). Seeing uniformity across a surface is logically equivalent to the absence of information for a gap. That is, at times what we call filling-in might be no more than a lack of neural signals for a physical discontinuity, ie nonisomorphic. A good example is the perception of a uniform brightness or colour change induced by a sawtooth-like luminance or chromatic variation in the Craik–O'Brien–Cornsweet illusion (Davey et al 1997; Wachtler and Wehrhahn, this issue). Distinguishing filling-in via signal propagation and not having neuronal information on a stimulus change requires careful controls. It might be interesting to extend the study of filling-in to include stimulus patterns with graded (Reid and Shapley 1988) or sparse, pointillistic inducing surrounds and targets (Singer and D'Zmura 1994; Jenness and Shevell 1995; Schirillo and Shevell 1996; Mausfeld 1998).

5 Filling-in via long horizontal connections

A physiological alternative to the computational model follows from findings suggesting that neurons responding to edges of one or another kind convey their information through intrinsic horizontal interactions to neurons whose receptive fields are uniformly illuminated by the enclosed area. Neurons that could mediate the perception of bright, coloured, and textured surfaces have been examined in a number of cortical visual areas from V1 to MT. Single-cell recordings made recently in cat striate cortex demonstrate that while there is no isomorphic representation of brightness in striate cortex, there appear to be scale-dependent lateral interactions, giving rise to a brightness representation (Rossi et al 1996). When a steady stimulus of uniform luminance was shown within the classical receptive field while the background luminance was modulated well beyond the receptive field area, the response of the neuron to the uniform stimulus could be modified (Paradiso et al 1996; Rossi et al 1996). This finding indicates long-range interactions between cortical neurons that bridge the size of local receptive fields.

How fast are the processes propagating information from one part (edge) to another (enclosed area)? Psychophysical experiments suggest that the horizontal interactions...
assumed to play a key role in the perception of surface brightness are relatively slow (Paradiso and Hahn 1996). Using a masking paradigm, Paradiso and Nakayama (1991) found that the enclosed area could be perceptually suppressed by a subsequent mask that was presented up to 100 ms later, suggesting that propagation is quite slow. Importantly, the latest time at which masking was effective increased with surface size, suggesting that there are progressive lateral interactions involved in mediating brightness. Additional support for the idea of a slow filling-in process comes from studies showing that brightness changes in the central area could only be induced if the frequency of surround modulation did not exceed 2.5 Hz (De Valois et al 1986). Furthermore, strength of induction declined with distance (Rossi and Paradiso 1996).

The slow propagation of contextual influences on brightness perception is reminiscent of the delayed response found neurophysiologically for other surface attributes of figure-ground segregation such as colour, motion, orientation, and texture contrast (De Weerd et al 1995; Sillito and Jones 1996; von der Heydt et al 1996; Zipser et al 1996). In agreement with the psychophysical findings, neuronal surface representation follows edge modulation by 20–30 ms (Lamme et al 1997). The laterally propagating signal (slow-distributed component) studied by Kitano and colleagues (1994, 1995) also peaks approximately 30 ms after the fast local field potential generated within the classical receptive field. Additionally, that signal does not follow high-frequency modulation of the stimulus.

Is there a known anatomical basis for these interactions? Gilbert and Wiesel (1992) in the monkey and Lund et al (1993) in the cat have provided evidence for long axonal connections capable of transmitting information from an edge to the inner section of an enclosed area. They also showed that the receptive field is not of fixed size, but can be ‘rewired’ within a few minutes by recruiting collaterals mediating inputs from nearby afferents, presumably through disinhibition. In their study a neuron whose receptive field had been photocoagulated resumed responding when neighbouring regions on the retina were illuminated. Effectively, this kind of remapping resulted in a much larger response area than before. Gilbert and Wiesel (1992) suggested that the structural and functional unit responsible for this kind of expansion can integrate subthreshold signals and group parts together by accessing cortical cell columns with similar orientation and colour preferences. The dynamic receptive field characterised by this type of interaction between spatially separate patches of retina reinforces Mach’s (1865) and Hering’s (1878) conclusion in the last century that knowing what is locally activated is not sufficient for predicting what is globally perceived.

It has been hypothesised by Gilbert (1992) that such a mechanism may form the basis for the perceptual filling-in of retinal and central scotomata (Teuber et al 1960; Eysel 1997); it may also explain the filling-in of an artificial scotoma, ie a uniform area on a differently coloured or textured background (Ramachandran and Gregory 1991). On a large scale, horizontal interactions of this kind might also lead to a better understanding of the induction of colour contrast, assimilation, neon colour and their relation to depth and transparency (van Tuijl 1975; Nakayama and Shimojo 1990; Nakayama et al 1990; de Weert and van Kruysbergen, preceding issue). Other examples in need of an explanation are the large-scale spreading of graininess and twinkle after adaptation to a dynamic noise field (Ramachandran and Gregory 1991; Spillmann and Kurtenbach 1992; Hardage and Tyler 1995); and the cooperative processes that are involved in contour and surface completion of densely textured surfaces, such as in random-dot stereograms and kinematograms (Frisby 1979; van de Grind et al 1983; Cavanagh 1987; Friedman et al 1996). Although these are fascinating ideas, we should be aware that in each case the time required for perceptual induction is shorter, by orders of magnitude, than the time for receptive field modification (Pessoa et al, forthcoming).
6 Grouping by distributed feedback from higher to lower levels

Global interactions would appear to require feedback mechanisms for their neurophysiological explanation. Accordingly, Hubel and Wiesel's (1962) concept of ascending hierarchical information processing was complemented by the idea of back-propagation from higher to lower cortical levels. Such modulation by higher-level inputs becomes plausible if one considers that layer IV neurons in visual area V1 of the monkey receive less than 10% of their excitatory input from retino-geniculate afferents (Peters et al. 1994); and that some cells in extrastriate areas V2 and V3 are almost completely silenced by inactivation of area MT (James et al 1997). One method by which feedback could be implemented is by using temporal synchronisation as a binding mechanism for grouping (Eckhorn et al 1988; Gray et al 1989; Singer 1993; Nelson 1995). Even though this concept remains controversial, it has opened the discussion to an understanding of how (pre-)cognitive influences may act on the ascending sensory input. In addition, it offers the possibility of testing explicit hypotheses about neural mechanisms subserving top–down processing (Tovee 1996).

One such test involves figure–ground segregation of a dotted figure on a static random-dot background. In the absence of relative motion the figure cannot be discerned. However, at the slightest movement, it will pop out according to the Gestalt principle of common fate. In experiments on motion processing in visual area MT of the behaving monkey, Newsome and Paré (1988) and Britten et al (1992) determined the threshold number of dots on a random-dot background required for a response to coherent motion. Thresholds obtained behaviourally and neurophysiologically in the same animal yielded very low percentages of dots and were statistically indistinguishable. These results strongly suggest that visual thresholds could be based on the activity of a relatively small number of neurons — directly linking the macroscopic and microscopic brain processes (Barlow 1972, 1994). More detailed mechanisms are likely to become known as neurophysiologists continue to probe the visual system using complex stimuli in trained alert monkeys (Stoner and Albright 1992).

7 Gestalt factors today

Meanwhile, a different approach emphasising the software, rather than the hardware (or wetware) of the visual system has been developed to account for the emergence of surfaces in complex patterns. One of the most spectacular demonstrations of local vs global processes in lightness perception is Cataliotti and Gilchrist's (1995) rendition of the Gelb effect. The stimulus is a staircase of five cardboard squares ranging from black to white. Initially, only the black square is presented in the beam of a spotlight — it appears white. As cardboard with successively higher reflectances are added to the row of squares, each square looks brighter than the former, which in turn appears darker. This effect is fairly independent of the distance between the squares, thus supporting a ratio approach or anchoring interpretation to brightness contrast (Wallach 1948; Gilchrist 1994) rather than an explanation by lateral inhibition. Another rediscovery pertains to Katz's (1911, 1930) fundamental distinction between transparent film colour (durchsichtige Flächenfarbe) and opaque surface colour (Oberflächenfarbe) in the study of shadows, ie a change of illumination versus a change of reflectance. No neuronal mechanisms have been proposed to account for these phenomena.

As to perceptual segregation, T-, X-, and L-junctions are being used to predict the relative brightness in complex patterns that may be seen in 2-D and 3-D (Kersten 1991; Watanabe and Cavanagh 1993; Pessoa and Ross 1996; Anderson 1997). Also, the appearance of a gray or coloured element has been demonstrated to depend on its perceptual grouping with other elements according to Gestalt organisation and common fate (Fuchs 1923; Koffka 1935; Agostini and Proffitt 1993). The Gestalt rule of good continuation finds its counterpart in research demonstrating the cardinal importance of collinear Gabor-type
and line stimuli for long-range contour mechanisms (Field et al 1993; Polat and Sagi 1993, 1994; Polat and Norcia 1996; Dresp and Grossberg 1997). Closure of long and smooth contours has been revived by the work of Kovacs and Julesz (1993; reviewed by Kovacs 1996), who used a chain of widely spaced elements embedded in a background of randomly oriented patches. Confirming the Gestalt credo that the whole is different from the sum of its parts (Koffka 1935), these authors found that segments could be more easily linked across large spatial distances when they belonged to a closed contour (global salience). This is a most promising new area in perceptual and computational vision research that would warrant treatment in a future special issue.

8 Outlook
The richness and variety of visual phenomena requiring global mechanisms for stimulus processing might serve as a sign to neuroreductionists that it is not sufficient to base an explanation on only one or two representative examples. By taking into account a wider range of variants of a given effect, we become quickly aware that our current knowledge of the neurophysiological basis of vision is far from complete (Uttal 1997). On the other hand, delighting in pure phenomenology without considering known physiological findings for constraining models of visual perception does not get us any closer towards understanding the underlying mechanisms.

In their special issue on perceptual organisation and object recognition, Wagemans and Kolinsky (1994) concluded that “If a general message is to be extracted...it is that the visual system’s processes cannot be characterised...by simple dichotomies such as analytic versus wholistic, bottom – up versus top – down, local versus global, low-level versus high-level, parallel versus serial” and that, instead, “...a wide variety of mechanisms is available to the visual system.” Apparently, what is being used for a given stimulus depends on the available information and the task. The rapidly expanding field of neuroimaging (Zeki 1993) should soon hold answers to some of these questions. Transcranial magnetic stimulation used to reversibly deactivate visual area MT and, as a consequence, motion perception (Beckers and Zeki 1995) has emerged as another exciting tool.

Where might the re-emergence of Gestalt approaches lead us? The field of vision research has moved in just the past two decades from an emphasis on filters (channels, spatial frequency, motion energy) to the study of contours, to the study of surfaces. Will the next step take us to the study of curved surfaces (Bülthoff 1991; Carman and Welch 1992; Kojo et al 1995) and representations that might subserve higher functions, such as object recognition? Behaviourist psychology, in the not-so-distant past attempted to reduce psychology to the study of observable behaviour, thereby denying the reality of subjective experience. However, it was inevitable that experience would eventually reassert itself as a valid domain of study, because this, after all, is what we wish to understand. The unique advantage of studying psychology is that we can make observations about our own experience that allow us to infer the nature of brain processes.

In rediscovering the Gestalt approach to the study of appearance, perhaps we will discover that the wholes or Gestalten of experience are not just surfaces, but higher-order representations, such as objects and events. But once we begin to conceive of perception in terms of meaningful objects and events, perception becomes much more than detection of stimuli via filters, or even of surface formation. It becomes a creative process of perceiving causality (Michotte 1946; Massironi and Bonaiuto 1966), intentionality (Heider and Simmel 1944; Minguzzi 1961), and meaning in the world (Gregory 1980; Shepard 1984; Rock 1987). Thus, psychology may be in the process of finding its rightful place as a bridge between the ‘two cultures’ (Snow 1959) of science and the humanities. In our attempts to understand the structure of experience and the processes of the brain that underlie that structure, our field is uniquely situated to help us understand ourselves.
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References (references to articles in this issue are not listed)
Adelson E H, Movshon J A, 1982 “Phenomenal coherence of moving visual patterns” Nature (London) 300 523–525
Agostini T, Proffitt D R, 1993 “Perceptual organization evokes simultaneous lightness contrast” Perception 22 263–272
Allman J, Miezin F, McGuinness E, 1985 “Stimulus specific responses from beyond the classical receptive field: Neurophysiological mechanisms for local – global comparisons in visual neurons” Annual Review of Neuroscience 8 407 – 430
Anderson B L, 1997 “A theory of illusory lightness and transparency in monocular and binocular images: the role of contour junctions” Perception 26 419–453
Anstis S M, 1986 “Movement perception in the frontal plane: Sensory aspects”, in Sensory Processes and Perception volume 1 of Handbook of Perception and Human Performance Eds K R Boff, L Kaufman, J P Thomas (New York: John Wiley) pp 16.1 – 16.27
Arrington K F, 1994 “The temporal dynamics of brightness filling-in” Vision Research 34 3371 – 3387
Bach M, Meigen T, 1997 “Similar electrophysiological correlates of texture segregation induced by luminance, orientation, motion, and stereo” Vision Research 37 1409 – 1414
Barlow H B, 1972 “Single units and sensation: a neuron doctrine for perceptual psychology?” Perception 1 371 – 394
Barlow H B, 1994 “The neuron doctrine in perception”, in The Cognitive Neurosciences Ed. M Gazzaniga (Cambridge, MA: MIT Press) pp 415 – 435
Baumann R, Zwaan R van der, Peterhans E, 1997 “Figure – ground segregation at contours: A neural mechanisms in the visual cortex of the alert monkey” European Journal of Neuroscience 9 1290 – 1303
Baumgartner G, Heydt R von der, Peterhans E, 1984 “Anomalous contours: a tool in studying the neurophysiology of vision” Experimental Brain Research Supplement 9, 413 – 419
Beckers G, Zeki S, 1995 “The consequences of inactivating areas V1 and V5 on visual motion perception” Brain 118 49 – 60
Békésy G von, 1968 “Mach- and Hering-type lateral inhibition in vision” Vision Research 8 1483 – 1499
Britten K H, Shadlen M N, Newsome W T, Movshon J A, 1992 “The analysis of visual motion: A comparison of neuronal and psychophysical performance” Journal of Neuroscience 12 4745–4765
Büthoff H H, 1991 “Shape from X: Psychophysics and computation”, in Computational Models of Visual Processing Eds M S Landy, J A Movshon (Cambridge, MA: MIT press) pp 305 – 330
Carman G J, Welch L, 1992 “Three-dimensional illusory contours and surfaces” Nature (London) 360 585 – 587
Cataliotti J, Gilchrist A L, 1995 “Local and global processes in lightness perception” Perception & Psychophysics 57 125 – 135
Cavanagh P, 1987 “Reconstructing the third dimension: Interactions between color, texture, motion, binocular disparity and shape” Computer Vision, Graphics and Image Processing 37 171 – 195
Chevreul M E, 1969 De la loi de contraste simultané des couleurs (Paris: Leon Laget) (original work published in 1839)
Cunningham D W, Shipley T F, Kellman P J, in press “Interactions between spatial and spatio-temporal information in spatiotemporal boundary formation” Perception & Psychophysics
Davey M P, Maddess T, Srinivasan M V, 1997 “Temporal analysis of the Craik – O’Brien – Cornsweet effect” Investigative Ophthalmology & Visual Science 38 (4) S453 (abstract 2127)
De Valois R L, Webster M A, De Valois K K, Lingelbach B, 1986 “Temporal properties of brightness and color induction” Vision Research 26 887 – 897
De Weerd P, Gattass R, Desimone R, Ungerleider L G, 1995 “Responses of cells in monkey visual cortex during perceptual filling-in of an artificial scotoma” Nature (London) 377 731 – 734
Dresp B, Grossberg S, 1997 “Contour integration across polarities and spatial gaps: From local contrast filtering to global grouping” Vision Research 37 913 – 924
Duffy C J, Wurtz R H, 1997 “Medial superior temporal area neurons respond to speed patterns in optic flow” Journal of Neuroscience 17 2839 – 2851
D'Zmura M, 1992 “Color constancy: surface color from changing illumination” Journal of the Optical Society of America A 9 490 – 493
Eckhorn R, Bauer R, Jordan W, Brosch M, Kruse W, Munk M, Reitboeck H J, 1988 “Coherent oscillations: a mechanism of feature linking in the visual cortex? Multiple electrode and correlation analysis in the cat” *Biological Cybernetics* **60** 121 – 130

Eysel U, 1997 “Perilesional cortical dysfunction and reorganization”, in *Brain Plasticity, Advances in Neurology* volume 73, Eds H-J Freund, B A Sabel, O W Witte (Philadelphia, PA: Lippincott-Raven) pp 195 – 206

Field D J, Hayes A, Hess R F, 1993 “Contour integration by the human visual system: Evidence for a local 'association field'” *Vision Research* **33** 173 – 193

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

Frisby J P, 1979 *Seeing: Illusion, Brain and Mind* (Oxford; Oxford University Press)

Fuchs W, 1923 “Experimentelle Untersuchungen iiber die Anderung von Farben unter dem Einfluss von Gestalten” *Zeitschrift fiir Psychologie* **92** 249 – 325

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

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

Gilchrist A L, 1994 “Absolute versus relative theories of lightness perception”, in *Lightness, Brightness and Transparency* Ed. A L Gilchrist (Hillsdale, NJ: Lawrence Erlbaum Associates) pp 1 – 34

Gove A, Grossberg S, Mingolla E, 1995 “Brightness perception, illusory contours, and cortico-geniculate feedback” *Visual Neuroscience* **12** 1027 – 1052

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

Gregory R L, 1980 “Perceptions as hypotheses” *Philosophical Transactions of the Royal Society of London, Series B* **290** 181 – 197

Grind A van de, Doorn A J van, Koenderink J J, 1983 “Detection of coherent movement in peripherally viewed random dot patterns” *Journal of the Optical Society of America* **73** 1674 – 1683

Grossberg S, 1984 “Outline of a theory of brightness, color, and form perception”, in *Trends in Mathematical Psychology* Eds E Degreef, J van Buggenhaut (Amsterdam: North-Holland) pp 59 – 86

Grossberg S, Mingolla E, 1985a “Neural dynamics of form perception: Boundary completion, illusory figures, and neon color spreading” *Psychological Review* **92** 173 – 211

Grossberg S, Mingolla E, 1985b “Neural dynamics of perceptual grouping: Texture, boundaries, and emergent segmentation” *Perception & Psychophysics* **38** 141 – 171

Grossberg S, Todorovic D, 1988 “Neural dynamics of 1-D and 2-D brightness perception: A unified model of classical and recent phenomena” *Perception & Psychophysics* **43** 241 – 277

Hardage L, Tyler C W, 1995 “Induced twinkle aftereffect as a probe of dynamic visual processing mechanisms” *Vision Research* **35** 757 – 766

Heider F, Simmel M, 1944 “A study of apparent behavior” *American Journal of Psychology* **57** 243 – 259

Heitger F, Roseenthaler L, Heydt R von der, Peterhans E, Kübler O, 1992 “Simulation of neural contour mechanisms: From simple to end-stopped cells” *Vision Research* **32** 963 – 981

Hering E, 1878 *Zur Lehre vom Lichtsinn* (Vienna: Gerold und Söhne) [Translation into English: Hurvich L M, Jameson D, 1964 *Outlines of a Theory of the Light Sense* (Cambridge, MA: Harvard University Press)]

Hess C, Pretori H, 1894 “Messende Untersuchungen über die Gesetzmässigkeit des simultanen Helligkeits-Contrastes” v. Graefe’s *Archiv für Ophthalmologie* **XL** 1 – 24

Heydt R von der, Zhou H, Friedman H, 1996 “Cortical coding of extended colored figures” *Perception* **25** Supplement 16 (abstract); *Investigative Ophthalmology & Visual Science* **37** (3) S904 (abstract 4180)

Hubel D H, Wiesel T N, 1962 “Receptive fields, binocular interaction and functional architecture in the cat’s visual cortex” *Journal of Physiology (London)* **160** 106 – 154

Hurvich L M, Jameson D, 1966 *The Perception of Brightness and Darkness* (Boston: Allyn & Bawn)

James A C, Hupe J-M, Payne B R, Lomber S G, Girard P, Bullier J, 1997 “Feedback connections from area MT gate information transfer in neurons of areas V1, V2 and V3”, in *Society for Neuroscience Abstract Volume* **23** p.1396 (abstract)

Jameson D, Hurvich L M, 1961 “Complexities of perceived brightness” *Science* **133** 174 – 179

Jenness J W, Shevell S K, 1995 “Color appearance with sparse chromatic context” *Vision Research* **35** 797 – 805

Kanizsa G, 1979 *Organization in Vision* (New York: Praeger)
Kapadia M K, Ito M, Gilbert C D, Westheimer G, 1995 “Improvement in visual sensitivity by changes in local context: parallel studies in human observers and in V1 of alert monkeys” Neuron 15 843 – 856
Kaplan G A, 1969 “Kinetic disruption of optical texture: The perception of depth at an edge” Perception & Psychophysics 6 193 – 198
Katz D, 1911 “Die Erscheinungsweisen der Farben und ihre Beeinflussung durch die individuelle Erfahrung” Zeitschrift für Psychologie, Ergänzungsband 7 (Leipzig: Barth) pp 6 – 31
Katz D, 1930 Die Erscheinungsweisen der Farben 2nd edition [Translation into English: MacLeod R B, Fox C W, 1935 The World of Colour (London: Kegan Paul)]
Kennedy J M, 1987 “Lo, perception abhors not a contradiction”, in The Perception of Illusory Contours Eds S Petry, G E Meyer (New York: Spinger) pp 253 – 261
Kersten D, 1991 “Transparency and the cooperative computation of scene attributes”, in Computational Models of Visual Processing Eds M S Landy, J A Movshon (Cambridge, MA: MIT Press) pp 209 – 228
Kitano M, Kasamatsu T, Norcia A M, Sutter E E, 1995 “Spatially distributed responses induced by contrast reversal in cat visual cortex” Experimental Brain Research 104 297 – 309
Kitano M, Niiyama K, Kasamatsu T, Sutter E E, Norcia A M, 1994 “Retinotopic and non-retinotopic field potentials in cat visual cortex” Visual Neuroscience 11 953 – 977
Koffka K, 1935 Principles of Gestalt Psychology (New York: Harcourt, Brace)
Kojo I V, Liinasuo M E, Rovamo J M, 1995 “Neon colour spreading in three-dimensional illusory objects” Investigative Ophthalmology & Visual Science 36 (4) S665 (abstract 3044)
Kovacs I, 1996 “Gestalten of today: early processing of visual contours and surfaces” Behavioural Brain Research 82 1 – 11
Kovacs I, Julesz B, 1993 “A closed curve is much more than an incomplete one: effect of closure on figure–ground segregation” Proceedings of the National Academy of Sciences of the USA 90 7495 – 7497
Lamme V A F, 1995 “The neurophysiology of figure–ground segregation in primary visual cortex” Journal of Neuroscience 15 1605 – 1615
Lamme V A F, Zipser K, Spekreijse H, 1997 “Figure–ground signals in V1 depend on extrastriate feedback” Investigative Ophthalmology & Visual Science 38 (4) S969 (abstract 4490)
Land E H, 1983 “Recent advances in retinex theory and some implications for cortical computations: color vision and the natural image” Proceedings of the National Academy of Sciences of the USA 80 5163 – 5169
Lappe M, Bremmer F, Pekel M, Thiele A, Hoffmann K P, 1996 “Optic flow processing in monkey STS: a theoretical and experimental approach” Journal of Neuroscience 16 6265 – 1985
Larimer J, Krantz D H, Cicerone C M, 1975 “Opponent process additivity. II. Yellow/blue equilibria and nonlinear models” Vision Research 15 723 – 731
Liebmann S, 1927 “Uber das Verhalten farbiger Formen bei Helligkeitsgleichheit von Figur und Grund” Psychologische Forschung 9 300 – 353 [Translation into English: West M, Spillmann L, Cavanagh P, Mollon J, Hamlin S, 1996 “Susanne Liebmann in the critical zone” Perception 25 1454 – 1495]
Lund J S, Yoshioka T, Levitt J B, 1993 “Comparison of intrinsic connectivity in different areas of macaque monkey cerebral cortex” Cerebral Cortex 3 148 – 162
McCann J J, 1987 “Local/global mechanisms for color constancy” Die Farbe 34 275 – 283
Mach E, 1865 “Über die Wirkung der räumlichen Verteilung des Lichtreizes auf der Netzhaut” Sitzungsberichte der kaiserlichen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Classe 52 303 – 322 [Translation into English: Ratliff F, 1965 Mach Bands: Quantitative Studies on Neural Networks in the Retina (San Francisco, CA: Holden-Day)]
Maloney L T, Wandell B A, 1986 “Color constancy: a method for recovering surface spectral reflectance” Journal of the Optical Society of America A 3 29 – 33
Massironi M, Bonaiuto P, 1966 “Ricerche sull’espressivita: qualita funzionali, intenzionali e relazioni di causalita in assenza di ‘movimento reale’” Rassegna di Psicologia Sperimentale e Clinica 8 1 – 42
Mausfeld R, 1998 “Color perception: From Grassmann codes to a dual code for object and illumination colours”, in Color Vision: Perspectives from Different Disciplines Eds W Backhaus, R Kliegl, J S Werner (Berlin: Walter de Gruyter) pp 219 – 250
Metelli F, 1974 “The perception of transparency” Scientific American 230 (4) 91 – 98
Metcalf R, 1932 Gesetze des Sehens second edition (Frankfurt a.M.: W Kramer) [third edition, 1975]
Michotte A, 1946 La Perception de la causalite (Louvain: Institut Supérieur de Philosophie) [Translation into English: Miles T R, Miles E, 1963 The Perception of Causality (London: Methuen)]
Minguzzi G, 1961 “Caratteri espressivi ed intenzionali dei movimenti: la percezione dell’attesa” Rivista di Psicologia Sperimentale e Clinica 8 1 – 42
Munsell R, 1957 A Color notations (New York: R. Munsell Color Co.)
Munsell R, 1960 A color order (New York: R. Munsell Color Co.)
Nakayama K, Shimojo S, 1990 “Toward a neural understanding of visual surface representation” Cold Spring Harbor Symposia on Quantitative Biology 55 911 – 924
Nakayama K, Shimojo S, Ramachandran V S, 1990 “Transparency: relation to depth, subjective contours, luminance, and neon color spreading” Perception 19 497 – 513
Nelson J I, 1995 “Binding in the visual system”, in Handbook of Brain Theory and Neural Networks Ed. M Arbib (Cambridge, MA: MIT Press) pp 157 – 159
Nelson J I, Frost B J, 1978 “Orientation-selective inhibition from beyond the classic visual receptive field” Brain Research 139 59 – 65
Nelson J I, Frost B J, 1985 “Intracortical facilitation among co-oriented, co-axially aligned simple cells in cat striate cortex” Journal of Experimental Brain Research 61 54 – 61
Newcombe W T, Paré E B, 1988 “A selective impairment of motion perception following lesions of the middle temporal visual area (MT)” Journal of Neuroscience 8 2201 – 2211
Nothdurft H C, 1993 “The role of features in preattentive vision: Comparison of orientation, motion and color cues” Vision Research 33 1937 – 1958
Paradiso M A, Hahn S, 1996 “Filling-in percepts produced by luminance modulation” Vision Research 36 2657 – 2663
Paradiso M A, Kim W, Nayak S, 1996 “Cortical representation of surface brightness: influences from beyond the classical receptive field”, in Society for Neuroscience Abstract Volume 22 p. 951 (abstract 376.6)
Paradiso M A, Nakayama K, 1991 “Brightness perception and filling-in” Vision Research 31 1221 – 1236
Pessoa L, Ross W D, 1996 “A contrast/filling-in model of 3-D lightness perception”, in Proceedings of the 9th Annual Conference on Neural Information Processing Systems (NIPS’95), Denver: Advances in Neural Information Processing Systems 8 Eds D Touretzky, M Mozer, M Hasselmo (Cambridge, MA: MIT Press) pp 844 – 850
Pessoa L, Thompson E, Noe A, forthcoming “Finding out about filling-in: A guide to perceptual completion for visual science and the philosophy of perception” Behavioral and Brain Sciences Peterhans E, Heydt R von der, 1989 “Mechanisms of contour perception in monkey visual cortex. II. Contours bridging gaps” Journal of Neuroscience 9 1749 – 1763
Peters A, Payne B R, Budd J A, 1994 “A numerical analysis of the geniculocortical input to striate cortex in the monkey” Cerebral Cortex 3 69 – 78
Polat U, Norcia A M, 1996 “Neurophysiological evidence for contrast dependent long-range facilitation and suppression in human visual cortex” Vision Research 36 2099 – 2109
Polat U, Sagi D, 1993 “Lateral interactions between spatial channels: suppression and facilitation revealed by lateral masking experiments” Vision Research 33 993 – 999
Polat U, Sagi D, 1994 “The architecture of perceptual spatial interactions” Vision Research 34 73 – 78
Qian N, Andersen R A, 1994 “Transparent motion perception as detection of unbalanced motion signals. II. Mechanisms of contour perception” Journal of Neuroscience 14 7367 – 7380
Ramachandran V S, 1992 “Perception: A biological perspective”, in Neural Networks for Vision Image Processing Eds G A Carpenter, S Grossberg (Cambridge, MA: MIT Press) pp 45 – 91
Ramachandran V S, Gregory R, 1991 “Perceptual filling in of artificial scotomas in human vision” Nature (London) 350 699 – 702
Reid R C, Shapley R, 1988 “Brightness induction by local contrast and the spatial dependence of assimilation” Vision Research 28 115 – 132
Rock I, 1987 “A problem solving approach to illusory contours”, in The Perception of Illusory Contours Eds S Petry, G E Meyer (New York: Springer) pp 62 – 70
Rossi A F, Paradiso M A, 1996 “Temporal limits of brightness induction and mechanisms of brightness perception” Vision Research 36 1391 – 1398
Rossi A F, Rittenhouse C D, Paradiso M A, 1996 “The representation of brightness in primary visual cortex” Science 273 1104 – 1107
Sary G, Vogels R, Kovacs G, Orban G A, 1995 “Responses of monkey inferior temporal neurons to luminance-, motion-, and texture-defined gratings” Journal of Neurophysiology 73 1341 – 1354
Schein S J, Desimone R, 1990 “Spectral properties of V4 neurons in the macaque” Journal of Neuroscience 10 3369 – 3389
Schiller P H, 1996 “On the specificity of neurons and visual areas” Behavioural Brain Research 76 21 – 35
Schirillo J A, Shevell S, 1996 “Brightness contrast from inhomogeneous surrounds” Vision Research 36 1783 – 1796
Shepard R N, 1984 “Ecological constraints on internal representation: Resonant kinematics of perceiving, imagining, thinking, and dreaming” Psychological Review 91 417 – 447
Shipley T F, Killman P J, 1994 “Spatiotemporal boundary formation: Boundary, form, and motion perception from transformations of surface elements” Journal of Experimental Psychology: General 123 3 – 20
