

Review article

# Gestalten of today: early processing of visual contours and surfaces

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Received 20 November 1995; revised 7 March 1996; accepted 7 March 1996

## Abstract

While much is known about the specialized, parallel processing streams of low-level vision that extract primary visual cues, there is only limited knowledge about the dynamic interactions between them. How are the fragments, caught by local analyzers, assembled together to provide us with a unified percept? How are local discontinuities in texture, motion or depth evaluated with respect to object boundaries and surface properties? These questions are presented within the framework of orientation-specific spatial interactions of early vision. Key observations of psychophysics, anatomy and neurophysiology on interactions of various spatial and temporal ranges are reviewed. Aspects of the functional architecture and possible neural substrates of local orientation-specific interactions are discussed, underlining their role in the integration of information across the visual field, and particularly in contour integration. Examples are provided demonstrating that global context, such as contour closure and figure-ground assignment, affects these local interactions. It is illustrated that figure-ground assignment is realized early in visual processing, and that the pattern of early interactions also brings about an effective and sparse coding of visual shape. Finally, it is concluded that the underlying functional architecture is not only dynamic and context dependent, but the pattern of connectivity depends as much on past experience as on actual stimulation.

**Keywords:** Visual perception; Visual cortex; Perceptual organization; Spatial interaction; Contour; Context; Medial axis

## 1. Introduction

*"If things are shaped may we conclude that the framework is not? And if it be not, whence comes this difference?"*  
K. Koffka ([44], 1935, p. 177).

*"The difference lies in the fact that the biological form suggests an action".* R. Thom, ([83], 1983, p. 266).

Vision can be viewed as one of our most capable pattern seeking, and pattern generating faculties. While the environment is composed of lumps of various shape and size, a certain kind of pattern formation in the brain — composed of mostly locally connected neurons — might be assumed to correspond to the environmental patterns when we perceive them. If we are to know what intrinsic patterns of the brain correspond to the extrinsic patterns of the world, how the intrinsic patterns are generated, and what a proper description of the intrinsic patterns should look like, we shall seek the answers to age-old questions: what are the units or elements of the intrinsic patterns; what connectivity rules

hold between them; and what is the exact nature of their interactions?

At the functional level, much is known about specialized, parallel processing streams of low-level vision that extract primary visual cues. There is substantial psychophysical research on local analysis of visual features in, e.g., stereo, motion and texture perception. Following the neurophysiological discoveries of the 1960s, knowledge has been accumulating about the smallest processing units — or the elements — of the visual cortex: about the parameter specificities of neuronal receptive fields, such as orientation selectivity, ocular dominance, wavelength and directional selectivity. However, there is only a limited understanding of how the fragments, caught by local analyzers, are assembled together to provide us with a unified percept; how local discontinuities in texture, motion or depth are evaluated with respect to the context of extended object boundaries and surface properties.

The purpose of this review is to display key observations of psychophysics, anatomy and neurophysiology with regard to context-dependent perceptual and neural

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interactions of various spatial and temporal ranges. A coherent assessment of these interactions can potentially provide us with a set of better understood principles of perceptual organization. However, we should be aware of the fragility of the present interpretations, and of the loose threads between the reported phenomena.

Among the many other possibilities, the discussion will be limited to those interactions that are believed to occur in the primary visual cortex (V1) between orientation-selective cells with small receptive fields. The majority of simple cells in V1 responds best to edges or bars of a particular orientation [29,30]. They sum the retinal input in an approximately linear fashion within their small receptive fields. These receptive fields exhibit alternate excitatory and inhibitory regions, resembling the shape of 2-dimensional Gabor functions (see, e.g., Fig. 1a). Simple cells are assumed to perform linear spatial filtering, which is the “groundwork for higher visual processes” [14]. Based on the correlation between psychophysical evidence on the properties of spatial filters and physiological data on receptive field properties in V1, we presume that the first cortical representation of the visual image is mediated by linear spatial filters, such as orientation-specific Gabor filters of different sizes. Since these filters are spatially localized, and respond to input coming from a limited retinal region, spatially extended image patterns involve interactions between them. It is these interactions that will be followed, ranging from the local ones between neighboring units, through long sequences (or chains), to those that express a quasi-global structure. Tied to psychophysically observed interactions, a few related aspects of the internal anatomy and physiology of the primary visual cortex will also be looked at.

Matching anatomical detail with function requires the application of a variety of methods. In recent years, the introduction of novel research methods, including the replacement of single bars and gratings by more complex stimulus patterns, helped to reveal some of the basic features of perceptual and neuronal interactions. Stimuli are composed of Gabor patches in the psychophysical experiments to be reviewed here. Gabor patches are sinusoidal luminance signals with gaussian envelopes (see e.g. Fig. 1a). Because they roughly model the receptive field structure of simple cells in V1, it is assumed that these stimuli can selectively activate a limited set of early cortical neurons.

In Section 2, some aspects of the functional architecture and possible neural substrates of local orientation specific interactions will be reviewed. In Section 3, examples of chain-interactions will be presented, and it will be demonstrated that the pattern of connectivity depends as much on past experience as on the actual stimulation, and that the architecture is not fixed, but dynamic and context dependent. In Section 4, further examples of context dependency will illustrate that not only figure—ground assignment is realized early in processing, but there is also an effective and sparse coding of visual shape there.

## 2. Local interactions

### 2.1. Psychophysically measured lateral interactions

The architecture and dynamics of lateral interactions between oriented spatial filters have been recently studied in a contrast masking paradigm by Polat and

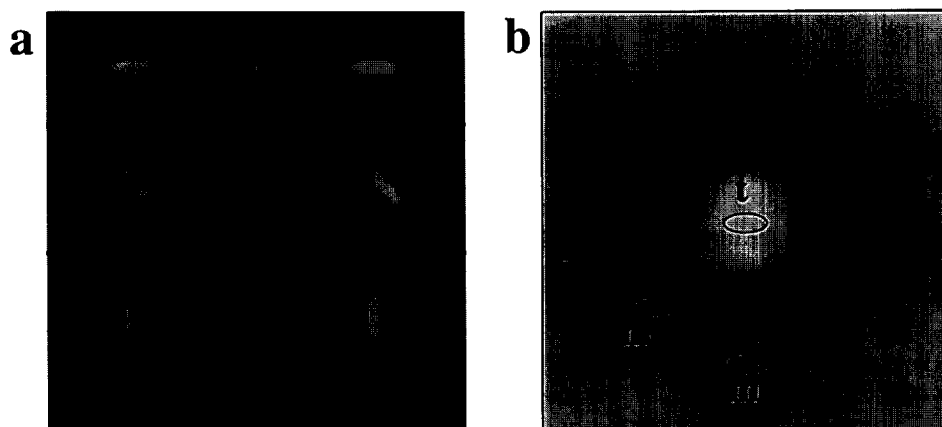


Fig. 1. Examples of stimulus patterns and results of psychophysical lateral masking experiments. a: the rows represent typical stimulus arrangements. The central Gabor patch (usually at threshold contrast) in each row is the target (t), and the two high-contrast flanking Gabors are the maskers (m). In these examples, target and maskers have the same orientation, and their relative arrangements are co-linear, diagonal and parallel, respectively. Contrast sensitivity was measured in each condition as a function of spatial separation between target and maskers. b: Gray-level map of contrast threshold variations for the stimulus conditions of a. Increased threshold is represented by light, reduced threshold by dark shading. The superimposed central ellipse indicates the target (t), and the others are maskers (m) at different locations. Note that 3 different regions emerge in the map: a central, nearly isotropic suppression region, and two separate enhancement regions. Enhancement is strongest in the co-linear arrangement (Results are replotted from Polat and Sagi [70]).

Sagi [70,71,90]. In this paradigm, local contrast sensitivity is measured for a foveal Gabor target in the presence of two 'masking' Gabor patches (see Fig. 1a). High contrast maskers produce a suppressive effect on threshold increase at close target-mask distances ( $0-1\lambda$ , where  $\lambda$  is the wavelength of the Gabor patches), and a threshold-reducing facilitatory effect at larger distances ( $2-6\lambda$ ) [70]. Facilitation is the strongest when the high contrast maskers and the target not only have similar orientation, but are aligned co-linearly, while suppression is more broadly tuned (Fig. 1b) [70,71]. Phase manipulations of the maskers serve to separate within filter, or 'direct', phase sensitive interactions, and 'indirect' interactions between non-overlapping filters, the latter being less sensitive for spatial phase [91]. Some of the orientation-selective interactions are preserved independently of mask phase, reflecting indirect interactions.

As illustrated in Fig. 1b, 3 fundamental interaction types emerge from the lateral masking studies: spatially short-range, non-linear, suppressive interactions; spatially longer range, 'side-way' orientation-selective facilitatory interactions (parallel arrangement of target and maskers); and particularly strong, orientation-selective facilitatory interactions, extending along the preferred orientation of the filters to large spatial distances (co-linear arrangement of target and maskers). Detection of texture borders might be mediated by the short-range type [79], and grouping and figure-ground segregation might be subserved by long-range facilitatory interactions [70]. Let us see how the longer range interactions are supported by the known connectivity of the brain.

## 2.2. Lateral connections in the primary visual cortex

The horizontal structure of the striate cortex is discernible when an extracellularly injected neural tracer (horse-radish peroxidase, HRP) is taken up by pyramidal neurons in layers 2 and 3A, labeling remote, periodically organized patches of neurons [74–77]. The HRP-labeled pattern resembles the stripes of a single orientation resulting from 2-deoxyglucose (2-DG) uptake in the cortex following visual stimulation with oriented lines [77]. Intracellularly injected HRP also reveals a patchy pattern of horizontal axonal arborization at the single cell level [23,24]. The patterns of intra- and extracellular HRP labeling are assumed to have a common origin, both revealing the extensive axonal collaterals of pyramidal cells that span several millimeters horizontally across the cortex (see an earlier review [86]).

It has been hypothesized that the functional role of these long axons is to connect cells with similar physiological properties, such as similar orientation preference [60]. This hypothesis has gained support from retrograde [25] and anterograde [41] anatomical labeling.

Optical imaging — combined with anatomical tracing techniques — not only indicates that horizontal connections link neurons with similar orientation preference [57], but also suggests that the connected cells are displaced in that same visuotopic direction [9,21].

The analysis of synaptic characteristics of horizontal connections reveals that the effect of long-range horizontal input can be both facilitatory or suppressive, depending on the balance of arriving inputs [28]. Among the target cells receiving long range input, the observed ratio of GABAergic inhibitory cells ranges between 5% (observed by electronmicroscopy in cat striate cortex [42]) and 20% (in macaque [59]). These figures suggest that the long lateral axons might subserve various types of intracortical interactions, but the majority of the postsynaptic effects is excitatory.

Some aspects of the relationship between horizontal connections and functional interactions were revealed by cross-correlation analysis. The observed interactions were excitatory, and occurred between like-oriented cells with non-overlapping receptive fields separated by several degrees [85]. More specific facilitatory interactions were also unveiled between co-oriented and co-axially aligned simple cells [62].

Although the plexus of long-range horizontal connections is only one (and already somewhat stereotypical) aspect of the internal anatomy of the primary visual cortex, it is significant enough to challenge the notion of restricted cortical receptive fields. In addition to 'direct' thalamic input, horizontal or 'indirect' input has the capacity to modulate the activity of cortical neurons. The most prevalent suggestion for the role of the long-range, orientation-specific facilitatory connections is that they permit integration of information between locations far from each other in the visual field [25]. Facilitation between co-oriented and co-axially aligned cells might be involved in the detection of long and smooth contours [62,21,9]. The aforementioned psychophysical lateral masking studies are consistent with this idea, revealing anisotropic excitatory interactions [64,71,70,91], that might subserve the integration of oriented segments into continuous contours.

In this section, some types and possible neural substrates of local orientation specific interactions are reviewed. Is the proposed architecture, with fixed connections between units, sufficient to accomplish visual segregation of extended objects? In the next sections more elements will be added to the list of simple pairwise interactions.

## 3. Chains of interactions

### 3.1. Perceived chains

Fig. 2 presents an example where long-range grouping processes help us to form a percept. A smooth 'snake'

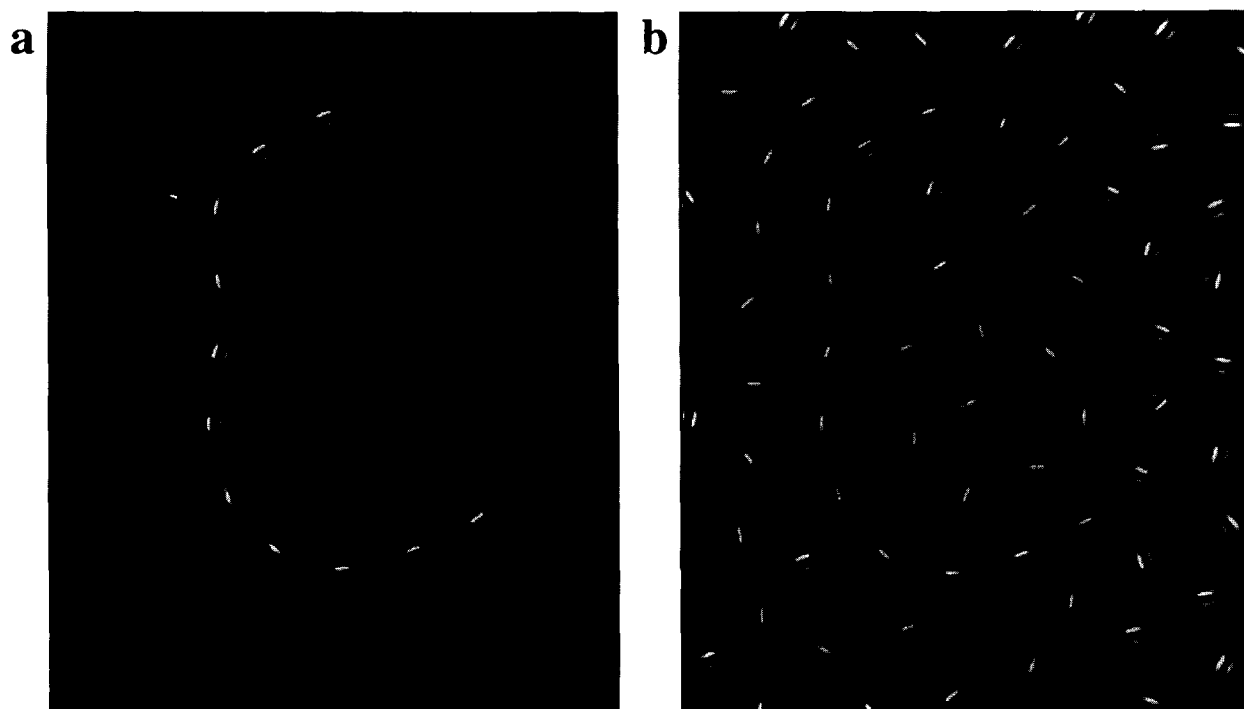


Fig. 2. Example of a Gabor-chain employed in contour detection experiments. a: a chain of roughly co-linearly aligned Gabor patches. b: the contour in a is embedded in a background of randomly positioned and oriented Gabor patches. In spite of the many other possibilities for grouping Gabor elements together, the contour still stands out (a similar example was given by Field et al. [20]).

in Fig. 2a is a chain of aligned Gabor patches. Although the snake is embedded in the background of randomly oriented and positioned segments in Fig. 2b, it is still perceivable. Primary cues cannot guide segmentation in Fig. 2b, because there are no gradients in basic feature domains, such as luminance, color or texture. This type of contour has been referred to as 'globally salient' [81]. It might be assumed that orientation-specific interactions in a locally connected network of orientation-selective units, preferring co-linear arrangements, mediates contour integration here. Psychophysical contour detection experiments support this suggestion. Field et al. [20] studied the local rules that govern the ability of human observers to detect contour continuity in images similar to Fig. 2b. Observers were able to see the chains at relatively large interelement spacings (larger than twice the size of the elements), but only up to  $\pm 30^\circ$  angular difference between the elements and the path. Field et al. interpret their results in terms of a local association field, resembling the one shown in Fig. 1b. The association-field integrates activity of non-overlapping filters with similar orientation tuning, predominantly along the filters' main orientation axes. The long-range horizontal axonal connections (mentioned in Section 2) are candidates for implementing the association-field. There is recent evidence for context-dependent spatial integration properties of primate V1 cells that are in agreement with psychophysical results, and support the role of within V1 interactions in contour salience [31].

### 3.2. Coupled chains

Note the several possibilities in Fig. 2b for linking segments together. There are chunks of nearly co-linear segments, and other neighbors are not co-linear but have similar orientations. Locally, any grouping rules (e.g., co-linearity or similarity) can be served by spatial interactions. Still, it is the long chain that pops out against the background, acquiring its global structure. Activity of orientation-selective units, or highly specific receptive fields sensitive to this particular contour cannot explain segregation. In fact, ambiguous solutions may arise even with the help of lateral interactions. The involved interactions that lead to global order have to carry information about mutual affiliation of the segments along the whole chain. In this respect, the snake is an illustrative instance of the so-called 'binding problem' (reviewed e.g. in [61]).

With respect to scene segmentation by neural networks, the binding problem has been addressed by asking how multiple segments of a coherent shape can be linked together while these segments are represented by neural activity at distributed locations in the brain [88]. It has been suggested that neurons responding to features of the same object are labeled by temporal correlation of their firing [1,2,88–90]. One type of temporal labeling can be implemented by oscillatory modulation of single cell activity. Stimulus-induced oscillations in the 40–50 Hz range are observed in the

primary visual cortex of cat by local field potential measurements and multiunit recordings [18,27,26] (reviewed in [19]). Synchronization of neuronal activity over more than 2 mm in cat cortex is reported to be always accompanied by oscillatory firing, while within short distances, oscillation might be absent [45].

It is hypothesized by many research groups that stimulus-specific synchronization of neural responses serves as a physiological mechanism for segmenting visual scenes; however, oscillatory modulation is not thought to be an exclusive solution for it (see e.g. [43,63]). As of yet, there is no direct evidence that relates the demonstrated contour integration capacities to temporal coding in the primate or human brain. Although the primary visual cortex is strongly affected by extracortical input and external input timing, layer IV neurons of V1 receive only 5–10% of their excitatory input from geniculocortical or 'direct' afferents [67,68]. Already in V1, the network of patchy horizontal and other intracortical excitatory connections form a functional architecture where internally driven synchronization might occur.

### 3.3. Plastic chains

Obviously, dealing with the 'everyday' task of segmentation, even synchronous firing has to be shaped according to the ever-changing input. This requires the links of the neural architecture to be dynamic, with modifiable connection strengths. The requirements include both rapidly arising and long-lasting modifications. Recent studies on low-level visual discrimination indicate that 'fast' and 'slow' learning might be mediated by different processes, the fast phase is probably being related to attentional filtering, and the slow phase requiring a long consolidation period [36–39]. However, it is still not a clarified question whether developmental plasticity (e.g. formation of cortical columns), experience-dependent long-term changes in the mature brain (e.g., skill learning), and transient changes in neural responsivity (e.g., perceptual adaptation, attentional modulation) share common mechanisms at the cellular level. At present, there is only little experimental indication for rapid modifications in the context of this paper. Perhaps, an account of the mechanisms of visual attention (for reviews see [10,16]) will provide us once with a better understanding of the fast dynamics of cortical interactions. On the other hand, there are several examples of enduring stimulus-specific changes in the adult visual cortex.

Let us examine the long-term stability vs. plasticity of connections as it is related to our earlier example in Section 2, where the rules of connectivity seemed to be settled. In the lateral masking paradigm (see Fig. 1), the maximal spatial range of interactions was about 6 times the wavelength of the Gabor signals. However, when

observers are trained in this task, the interaction range increases by even a factor of 3 [72,73,80]. This practice effect is specific for eye, orientation, spatial frequency and retinal position, indicating that the involved plasticity occurs within the primary visual cortex. An important finding in this paradigm is that practice-induced long-range interactions critically depend on intermediate connections: practicing has to go step-by-step, from short to larger target-mask separations, thereby strengthening, and 'chaining together' local, short-range connections [72]. It has recently been demonstrated that 'unlearning' of stabilized connections can also occur, as directed by task requirements [82]. The results suggest that learning is mediated by chains of connections between spatial filters, where the connections are modified by Hebbian associative rules. Cascades of these local, modifiable connections are thought to serve our ability to detect long-range signal correlations, and to establish high order associations.

Synaptic changes [22] and axonal sprouting [13] of long-range horizontal axonal connections were suggested to play a role in topographic reorganization phenomena in the mature primary visual cortex. When afferent cortical input is removed by small retinal lesions, the initially silenced cortical sites soon recover their activity, and enlargement and positional shift of receptive fields is observed [13,34]. Although the time required for these phenomena to occur is in the weeks or months range, recent psychophysical experiments using artificial scotomas suggest that they can happen even within a second [35]. It is suggested that dynamic receptive field alterations are part of normal visual processing and adaptation in the adult brain [11,40,69,87], although this seems to be one of the hottest controversial issues of neurophysiology [15].

With these examples of chains, I wished to demonstrate that the architecture of orientation-specific pairwise interactions, as described in Section 2, might not be enough to explain even such a simple perceptual event as contour integration. The pattern of connectivity depends as much on past experience as on the actual stimulation. Thus the functional architecture cannot be fixed, it is dynamic and context dependent. Let us see more details about contextual effects.

## 4. Global interactions

### 4.1. Closed chains

There is an embedded contour both in Figs. 3a and b. The one in Fig. 3b is easily seen; however, only close inspection reveals the other in 3a. Spacing between the segments is larger than it was in Fig. 2b, however, the angular and spatial separation between adjacent segments is the same along these contours, thus the contours

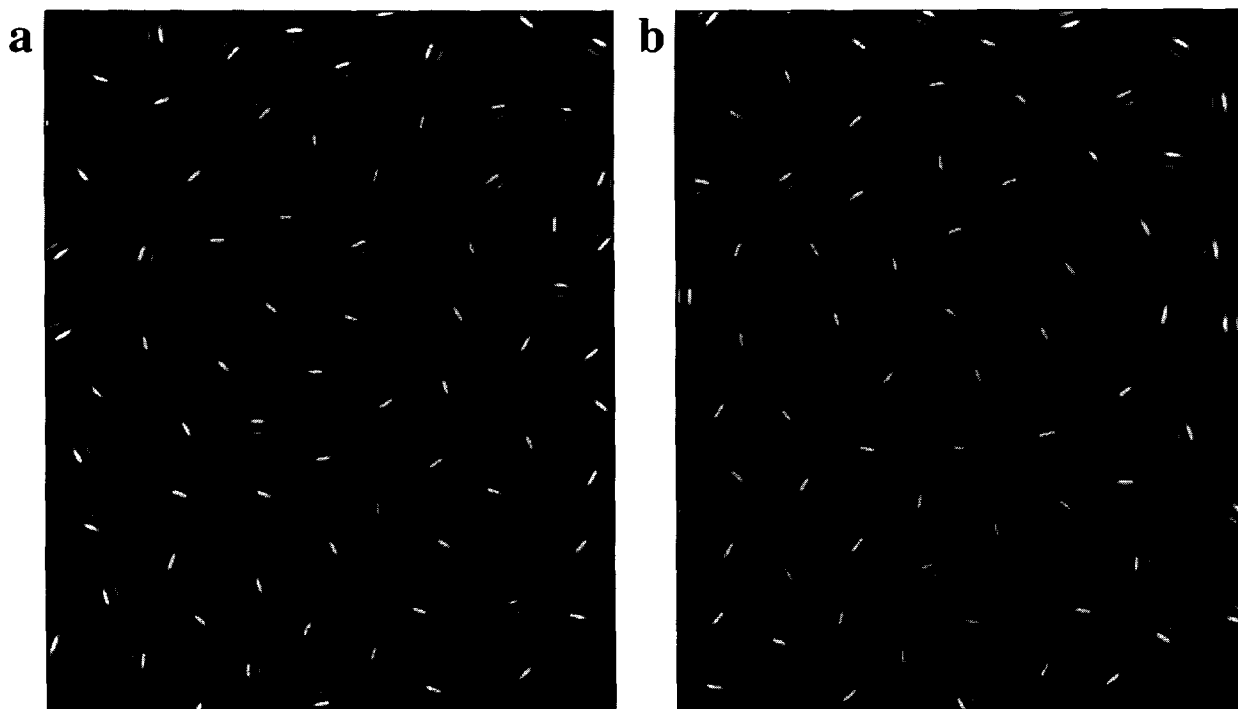


Fig. 3. Example of an open (a) and a closed (b) Gabor-chain. Spacing between adjacent segments is larger than that of in Fig. 2b, but is the same for both contours in the present example. At this spacing, only the closed contour is salient, and the elements of the open chain blend in the background, demonstrating the closure-superiority effect.

of Figs. 3a and b are locally equivalent. None of the previously discussed quasi-local aspects of vision would predict different sensitivity for these cases. The contours differ only in a global shape property which is closure. The quantitative difference between open and closed contours in terms of maximal gap-size was revealed in psychophysical contour detection experiments [47]. Closed contours are still salient at  $6\lambda$  gap size, while at gap size  $>3.3\lambda$  the open contours blend in the background. When a single segment is removed from the closed loop at maximal gap size, the contour is not perceivable any more [47], demonstrating that enhanced sensitivity is indeed due to closure and not produced by other stimulus properties. The 'closure superiority' effect is striking, because the global constraint of closure affects local association rules: adjacent, nearly co-linear segments can be linked across larger spatial distances when they belong to a closed contour.

Intuitively, local linking should be carried out before any global property is encountered. How can local detectors appreciate that they are parts of a whole? What mechanism of early vision can provide that? It might be speculated that reverberating circles of the Hebbian-type are behind closure superiority: propagation of a synchronous volley of neuronal firing might be arrested at the end of an open contour; however, when the contour is closed, and it is assumed that it has a 'closed' projection in the visual cortex, activity might flow around for a long time (which can also be called

short-term memory). Although this conjecture has not been tested directly, and particularly not in the primary visual cortex, there is experimental evidence for self-exciting cell assemblies in higher cortical regions. Reverberating synfire chains (first described in [1]) are believed to produce repeating multineuron patterns that are observed in the frontal cortex of behaving monkeys [3]. The synfire chain might be regarded as a general case of phase-locked oscillation, and although both has the capacity to bind distributed processes in the brain, as of yet, neither of them were convincingly demonstrated in primate visual cortex.

#### 4.2. Pruned chains

Coincident activity of many interacting neural elements can be revealed by tracing the activity of several units simultaneously, and searching for their higher order correlations, such as in electrophysiological cross-correlation and multiunit studies. Another alternative is to estimate how the activity of one unit is affected in the context of the activity of other units. In this reverse mapping technique, repeated application of stimulus patterns generates relatively stable neural interaction patterns, that can be mapped on to the local activity of single units.

We introduced the reverse mapping technique in psychophysical experiments to examine the global interaction pattern of a large number of local spatial filters

[46–49]. We measured local differential contrast thresholds of human observers for a single Gabor target that was surrounded by a background of randomly oriented and positioned Gabor patches and by a contour, forming different shapes. Spatial continuity across gaps defined the path of the contour, as it is shown in Fig. 3b. Contrast sensitivity maps of different shapes were obtained by measuring thresholds at different relative target-contour distances (see Fig. 4a). In other words, the shapes were moved around the target, and in separate experiments, contrast thresholds were estimated for a large number of locations within and outside of the shapes. Contrast thresholds on each of these locations were compared to the baseline threshold that was estimated in the absence of the contour. The difference between baseline and actual threshold was plotted, resulting in an activity surface (or sensitivity map) for each shape with valleys and peaks of sensitivity change (Fig. 4b). Note, that the method is similar to the one employed in lateral masking experiments (see Sections 2 and 3), except that the context (or ‘masker’) is more complex in the reverse mapping technique.

Two separate regions can be observed in the sensitivity map of Fig. 4b: one is related to the boundary and the other is related to the region bounded by the contour [46–49]. At short spatial distances from the contour, sensitivity change is similar to detection threshold variations in the paradigm of lateral masking. Sensitivity is reduced when target and contour overlap; and a facilitatory effect occurs symmetrically on both sides of the contour with peaks at  $2\lambda$  distance from the perimeter (for comparison, see Fig. 1b). The short-range effects can be interpreted by within-filter interactions. The second enhancement region is far from the perimeter, and can only be observed within the contour. The interior specific long-range effect suggests that ‘inside’ and ‘outside’

regions, or ‘figure’ and ‘ground’ are distinguished at the level where the measured variations in contrast sensitivity occur: it is assumed that psychophysical contrast thresholds for Gabor targets reflect the activity level of localized, early detector units, such as simple cells in V1. Observations, analogous to the present results, were reported in the primary visual cortex of the macaque monkey, where a strong asymmetry was found in single cells’ responses depending on whether the receptive field was positioned inside or outside of a figure [51,52,55,92,93]. These results were obtained with the reverse mapping technique applied in neurophysiology, where texture, motion, color or disparity defined figures were flashed at different spatial locations relative to the V1 cell’s classical receptive field position.

Because the central enhancement in Fig. 4b was not only interior specific, but it also exhibited a well-localized peak, it was decided to test whether the location of the peak would depend on the shape of the contour [48]. It was found that the internal peaks are in fact defined by shape and that they have an interesting symmetric property: the peaks occur on those locations that are equidistant from the majority of the boundary points (see Figs. 4b and 5a, b). Kovács and Julesz suggested [48,49] that the internal peaks correspond to the major quench points of a ‘grassfire’-like transformation [5–8,56,65,66]. This transformation reduces shapes into skeletons (medial axis or stick figure), and captures important invariants and global image properties. Psychophysical sensitivity maps of circular and ellipse contours [48] and of shapes with corners and concavities [50] indicate the presence of a skeletal transformation in human visual processing (see [12] for further psychophysical support related to the medial axis representation). Neural correlates of shape-specific sensitivity maps were recently found in the modulation profiles of single-

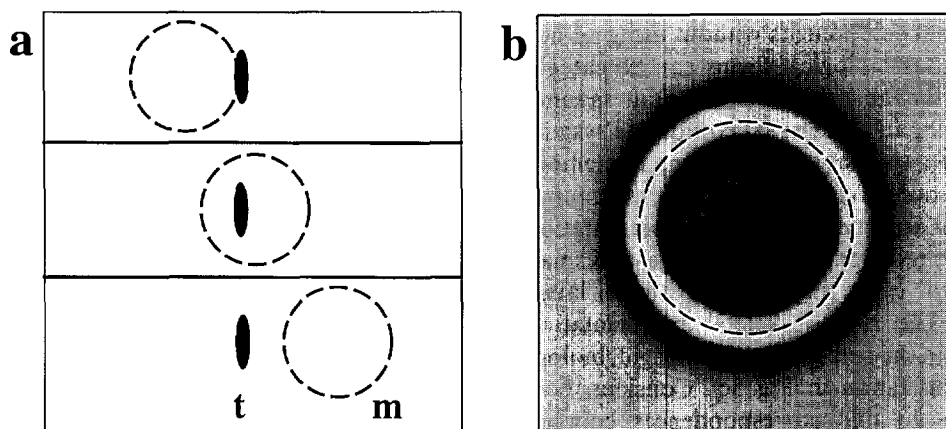


Fig. 4. The reverse mapping technique, and an example of a psychophysical sensitivity map. a: each row represents different relative target-contour distance conditions. In these experiments, differential contrast sensitivity of human observers was measured for a central Gabor target (t) in the presence of a closed contour (or masker (m)), and random noise. Contour and noise were similar to those of in Fig. 2b. Sampling included both within-figure and outside-figure target locations. b: psychophysical sensitivity map of a circular contour. Dark shading represents sensitivity enhancement, and light shading suppression. Note the sharp peak at the center of the circle (results are replotted from Kovács and Julesz [47]).

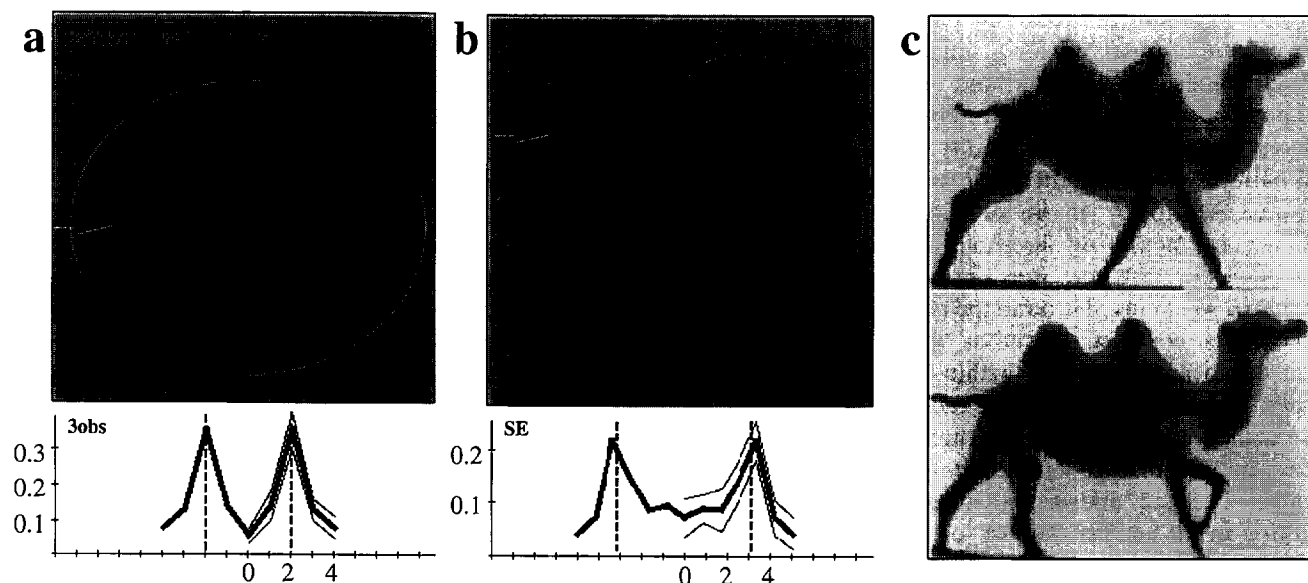


Fig. 5. Skeletal representation of different shapes. Our algorithm that computes the skeleton is based on an equidistance metric: the percentage of equidistant boundary points is computed for each internal point within the shapes, and the result is plotted in 2-D. In the upper panels of a–c, dark shading corresponds to the skeleton within the computed equidistance maps. Note that the skeleton is not uniform. The high amplitude, dark ‘hot-spots’ are equidistant from the longest segments of the boundary, indicating centers of high curvature. a: there are two major skeletal points within an ellipse (upper panel). The lower graph presents psychophysical results obtained with the reverse mapping technique. Sensitivity change is shown across the long axis of the ellipse, and it is expressed in log units. On the abscissa, distance from the center of the ellipse is expressed in  $\lambda$  units. Dashed lines correspond to the predicted peak locations. b: same as in a for a cardioid shape. Sensitivity change is well predicted by the equidistance metric. c: an advantage of the skeletal representation is that the original image can be reduced to a small number of dots (or ‘hot-spots’), that can be followed easily between frames of, for instance, a biological motion sequence.

cell activity in the primate striate cortex [53–55], employing the reversed-mapping technique. The neuronal correlates suggest an early cortical locus for our long-range, interior-, and shape-specific interactions.

It is possible that lateral interactions — behind the observed sensitivity maps — play crucial roles in figure synthesis, shape analysis, and extraction of simple spatial relations. The most provocative possibility is that an explicit skeletal representation of shape is generated early in visual processing. The skeletal representation can define constituent components without using ad hoc primitives; amorphous biological forms can be categorized in a translation and rotation invariant manner since it does not bring in an external coordinate system; and it seems to be an optimal way for coding in memory and to form associations. With respect to neural computation, an important aspect of the skeletal representation is that it reduces the redundancy of the image, and small cell assemblies can carry information about large, extended objects. The sparse skeletal representation might be employed in the perception of non-rigid, biological motion (see illustration in Fig. 5c). Consider, how costly it would be to find correspondences between sequential image frames of a moving figure if all the boundary points would have to be followed. I propose that the major skeletal points (such as the peaks in the sensitivity maps, or the darkest spots in Fig. 5c) are better alternatives for that kind of computation. Let us

note, that a similar proposal has been put forward by Marey in 1867 [58] and more recently by Johansson [33], but they have not considered the role of the medial axis representation in finding the proper locations for the points to follow.

In this last section it is shown that contour closure enhances local interactions. It is not yet known how closure superiority comes about. It might be a result of reverberating neural activity within a single layer of the visual cortex, or it might as well be a result of interactions between lower and higher levels of processing. However, the closure superiority effect helped in realizing the significance of contextual effects in local interactions, and it was learned that a closed line is not simply a chain of segments, it is a bounding contour that encloses the figure. The sensitivity maps proved that figure–ground relationships affect local interactions, since local contrast sensitivity is affected by them. An unexpected finding was that not only figure–ground assignments are realized early in processing, but there also is an effective and sparse shape-coding representation there. It is a rare coincidence that psychophysics and neurophysiology support this issue simultaneously.

## 5. Summary

A few types and the possible neural substrates of local orientation-specific interactions have been reviewed,



emphasizing their role in the integration of information across the visual field, and in particular in contour integration. It was also demonstrated that the pattern of connectivity depends as much on past experience as on actual stimulation, and — as interesting instances of contextual effects — it was shown that contour closure and figure–ground relations affect local interactions. Thus, the functional architecture does not seem to be fixed, it is dynamic and context dependent.

How do we stand today in the attempts of the Gestalt school to explain the principles of perceptual organization? In 1935, Koffka proposed: “If a line forms a closed, or almost closed, figure, we see no longer merely a line on a homogeneous background, but a surface figure bounded by the line. This fact is so familiar that unfortunately it has, to my knowledge, never been made a subject of special investigation. And yet it is a very startling fact, once we strip it of its familiarity” ([44], p. 150). Fig. 3 in the present paper, and the related contour detection experiments [47] attest Koffka’s idea in modern terms. The closure superiority effect demonstrates that local detectors of low-level vision appreciate that they are parts of a whole, or, as Koffka would say: “the process of organization depends upon the properties of its result” ([44], p. 151). However, it is still not exactly known which mechanism, out of the mechanisms reviewed, or some others, can provide that. One way to proceed is to seek what the gestaltists sought for: “we want a functional proof for our claim that a figure surrounded by contours is an entity different from the field outside the contours, which in all other respects produces the same stimulation... We might measure the threshold of a small figure produced either inside or outside the contour of our original figure... Unfortunately this experiment has never been made” says Koffka ([44], p. 150). Fortunately, the reverse-mapping technique, described in Section 4.2, provides a good tool to carry out this experiment, and to obtain the first experimental probe for global image properties. It has been shown with psychophysical reverse mapping that visual detection is enhanced when a target is positioned within a closed contour [46–50]. Correlates of such figure–ground effects have been recently found in the primary visual cortex using physiological reverse-mapping techniques [51–55,92,93]. “The results show that context modulation within primary visual cortex has a highly sophisticated nature, putting the image features the cells are responding to into their fully evaluated perceptual context” ([52], p. 1605). Some of these new studies extend the classical notions of shape and ‘prägnanz’ beyond the Gestalt psychoneural isomorphism: the sensitivity maps not only show context dependency, but also provide evidence for a medial axis-type transformation [48–50,53–55], which offers a continuous dialog between memory and stimulus [8], and offers invariant measures of shape for coding and action.

These examples illustrate that already the simplest units of the cortical architecture — neurons in the primary visual cortex — change their stimulus-response characteristics depending on the global stimulus structure. What are the general implications of that for today’s biology? Feature-based theories of perception can hardly predict the self-organizing, cooperative interactions that expose themselves in the sensitivity maps, just as the germ theory of disease cannot predict different sensitivity of individuals to infections [17]. The gestaltists of cell biology have long suggested that it is the physiological imbalance of the host organism that provides the context for microorganisms to cause troubles: “the disease is essentially the result of the host’s response” ([84], p. 170), not of the germs per se. Long forgotten experiments demonstrate that different bacterial strains, when they are cultivated in the same type of medium, can become identical ([78] as cited in [32]); and vice versa, a certain type of bacterium, say, a chain-structured coccus (*Streptococcus*) can take the shape of different classes (those of including more/less pathogens for man) depending on the type of different media it is cultured in [4]. It seems that these essential micro-entities, neurons or bacteria, that are believed to have some fixed properties, are in fact constantly changing according to the actual environment or context. The consequences are important in both cases: we ought to handle these entities in a way that optimizes and not restricts their functioning. The capacities of neurons will reveal themselves when neurons are given the type of stimulation they have evolved for; and microbes will function on our side when they find the proper biochemical environment within us. The desirable strategy is to provide the right conditions for the formation of ‘shape’ and observe our capability to generate (or ruin) coherent patterns in any domain.

### Acknowledgement

I thank Ákos Fehér for providing his inventive method to compute the medial axis transformation, Harry Schick for bringing into my view long forgotten facts of cell biology, Karl Zipser and Tai Sing Lee for facilitating discussions on the neurophysiology of the primary visual cortex, Thomas V. Papathomas, Eileen Kowler, Bela Julesz, and two anonymous reviewers for their helpful comments on the manuscript. Preparation of this paper was supported by a grant from the National Science Foundation and OTKA (U.S.-Hungarian Science and Technology Joint Fund JF-360).

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