Functional architecture of long-range perceptual interactions

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Abstract—The pattern of lateral interactions in the primary visual cortex, which has emerged from recent studies, conforms to the grouping rules of similarity, proximity, smoothness and closure. The goal of this paper is to understand the perceptual salience of oriented elements that are specifically organized to form a smooth contour. An overview of recent studies, in combination with new experimental results, is presented here to emphasize the idea that visual responses depend on input from both the center and the surround of the classical receptive field (CRF). It is assumed that normal lateral interactions produce a neuronal network that is formed by two antagonistic mechanisms: (i) excitation, that is spatially organized along the optimal orientation (collinear), and is predominant near the contrast threshold of the neuron, and (ii) inhibition, that is less selective and is distributed diffusely around the cell’s response field. Thus, the inputs from the CRF and the anisotropic surround are summated non-linearly. The specificity of the facilitation and suppression along the collinear direction suggests the existence of second-order elongated collinear filters, which may increase the response similarity between neurons responding to elongated stimulus, thus may enhance the perceptual salience of anisotropic configurations such as contours. This causal connection is particularly evident in amblyopes, where abnormal development of the network results in the abnormal perception of contours.

BACKGROUND

The visual system can detect small, local luminance differences (contrast) and group them into behaviorally relevant objects. The local processes are context-dependent and require integration between remote image parts. According to the Gestalt theory of perception, the visual system groups features together (the whole is different from its parts and is a non-linear process) on the basis of similarity, proximity, smoothness, closure, common region and connectedness (for review see Rock and Palmer, 1990; Spillmann, 1997). The grouping effect is assumed to operate at a very early (pre-attentive) stage of processing, without involving attention. Lateral interactions in the primary visual cortex are found even under conditions presented
without attention in anesthetized cats (Polat et al., 1998). These interactions, along with feedforward and feedback connections, are believed to mediate the grouping process. Under certain conditions, like similarity (same orientation), smoothness (collinearity), and proximity (target-flankers separation), the non-linear interactions act to integrate small oriented textures into elongated collinear contours. We postulate that these normal lateral interactions produce a selective neuronal network of excitatory (amplification) and inhibitory (de-amplification) interactions that are capable of controlling the perceptual grouping. When the ‘context’ of a stimulus satisfy the Gestalt rules, the network act to enhance the perception of this stimulus, whereas, when the ‘context’ does not satisfies these rules, the network does not enhance the grouping of the stimulus.

THE STANDARD MODEL OF SPATIAL VISION

According to the classical view of the organization of the visual cortex, neurons mediate visual information from the retina to the visual cortex through a few successive stages, while each stage elaborates on the feature selectivity developed at earlier stages (Hubel and Wiesel, 1968). In this view classical receptive fields (CRF) of simple cells, which have been tuned selectively for location, orientation and spatial frequency, form the fundamental units of analysis (for review see De Valois and De Valois, 1990). The standard model of spatial vision postulates that every image location is represented by population of linear spatial filters selective for different orientations and spatial frequencies. In spite of the finding that cortical simple cells may have more than 2–3 subregions (Mullikin et al., 1984; De Valois et al., 1985) it has been suggested that the weighting functions of spatial filters that most resemble those of cortical simple cells have 2–3 antagonistic spatial subunits (Watson, 1982; Watson et al., 1983; Klein and Levi, 1985; Wilson, 1986). In these models the outputs of linear spatial filters produce a field of local signals that can be integrated at later stages of signal processing (Wilson, 1991; Wilson and Wilkinson, 1997).

CONTRAST RESPONSE FUNCTION

Contrast is one of the most important attributes of the visual stimulus and determines visual neuronal response. The contrast response function in the cellular and perceptual levels, which has been a subject of intensive theoretical and experimental interest, is generally described as a sigmoid non-linearity that accelerates for small filter responses and compresses for large filter responses. The accelerating non-linearity at low contrast is usually termed a contrast threshold. Note that in spite of using the same term, the contrast threshold of neurons is determined by the shape of the function and that of humans is determined by a behavioral criterion (75–80%
correct). Most knowledge about early mechanisms in vision is based on threshold data, since the threshold is best suited for exploring independent mechanisms.

Contrast threshold is determined also by lateral interactions in the visual cortex. The contrast threshold and the response function of the local filters (neurons) in the primary visual cortex are context-dependent and can be modulated by remote image parts. The shape of the contrast response function may be changed according to context modulations (Polat et al., 1998; Sengpiel et al., 1998). Under collinear interactions, change of the slope was observed and under cross-orientation suppression rightward shift was observed. Context dependency was observed in psychophysical studies (Polat and Sagi, 1993, 1994a, b; Bonneh and Sagi, 1998), in visual evoked potentials (VEP, Polat and Norcia, 1996) and in single-unit recordings in cats and monkeys (Kapadia et al., 1995; Sillito et al., 1995; Levitt and Lund, 1997; Polat et al., 1998a; Sengpiel, 1998). Moreover, tasks involving visual imagery (Ishai and Sagi, 1997) and short-term memory (Tanaka and Sagi, 1998) also modulated the contrast threshold, suggesting the involvement of feedback from higher levels.

The contrast threshold for a Gabor patch can be enhanced or suppressed by the lateral placement of other Gabor patches of similar orientation and spatial frequency (Polat and Sagi, 1993, 1994a, b). In Fig. 1 we re-plotted data from such experiments. There are two zones, suppression and facilitation, where contrast detection thresholds are affected by flanking Gabor patches. The sign of the effect depends on the separation of the target and flanks, on the relative orientation of the flanks and on the global configuration of the three Gabor patches. Collinear configurations were found to produce maximal contrast facilitation (Polat and Sagi, 1993, 1994a, b; Polat and Norcia, 1996; Polat et al., 1998a).

![Figure 1. Lateral interactions. Typical figure as described in Polat and Sagi (1993, 1994a, b) and herein in Fig. 3A. Observers detected a Gabor target flanked by two high-contrast collinear Gabor signals at different distances. Contrast detection thresholds relative to the absolute threshold (no flanks) are plotted as a function of the target to mask distance in Gabor wavelength units (λ). The real stimulus of Gabor patches used in these experiments is presented (Polat and Sagi, 1993, 1994a, b).](image-url)
THE IMPORTANCE OF THE COLLINEAR CONFIGURATIONS

The facilitation of the contrast threshold for the collinear configurations, by the remote high contrast flankers, may suggest that contrast is summating preferentially along the collinear configurations at threshold (Polat and Norcia, 1997; Polat and Tyler, 1999). These studies measured the contrast detection threshold for elongated Gabor targets. The orientation of the carrier was either the same as that of the patch envelope (collinear) or orthogonal to it (see icons in Fig. 2). The contrast threshold improved for elongated configurations that were collinear with the grating bars (see Fig. 2). These results are consistent with configuration-dependent summation being more extensive along the axis of orientation. Polat and Tyler (1999) found that the improvement of the contrast threshold might be explained by filters elongated up to about 4 cycles.

FIRST OR SECOND-ORDER FILTERS?

The threshold facilitation along elongated collinear configurations could be either from within elongated linear filters or from collinear elongated non-linear integrating filters (second-order). The experiments of Polat and Tyler (1999) did not test the effects of contrast integration within the linear filter and therefore couldn’t differentiate between the two possibilities.

![Figure 2. Elongated filters and collinear fields of interactions. The observers in these experiments showed improved summation along the collinear configuration; however, the estimation of the optimal filter was longer then the other observers, in this experience observer, which suggests the involvement of practice in shaping the spatial filters. Modified from Polat and Tyler (1999). The real stimulus of Gabor patches used in these experiments is presented in (Polat and Norcia, 1998; Polat and Tyler, 1999).](image-url)
Linear filters are sensitive to the contrast phase of the stimulus, an effect that can be used to estimate the shape of the linear filters. Much evidence has suggested that when the Gabor flankers are positioned at a target-flanker separation of 2–3 cycles, the pooling of collinear targets is independent of the contrast phase (Polat and Sagi, 1993; Zenger and Sagi, 1996; Ishai and Sagi, 1997; Chen and Tyler, 1998). This effect was found when the flankers were at suprathreshold (Polat and Sagi, 1993; Zenger and Sagi, 1996; Ishai and Sagi, 1997) or at threshold contrast (Chen and Tyler, 1998). Facilitation of collinear line segments is also independent of contrast polarity (Wehrhahn and Dresp, 1988). Therefore, the improved collinear summation above 3 cycles (Polat and Norcia, 1998; Polat and Tyler, 1999) would probably need to be mediated by elongated second-order filters.

Contrast discrimination is non-linear when the stimulus signal is displayed on a contrast pedestal. As pedestal contrast increases, the threshold decreases first (facilitation) and then increases (suppression). This response is known as a dipper function (Legge and Foley, 1980; Ross et al., 1993; Zenger and Sagi, 1996).

The facilitation near the contrast threshold and suppression at suprathreshold contrast revealed from the long-range interactions are qualitatively reminiscent of the transducer function, and can be described as a dipper function (Morgan and Dresp, 1995). According to this view, the inputs from the high-contrast flankers and the near threshold target are added linearly to exceed the threshold. Thus the effect of facilitation revealed from superimposed pedestal and from laterally separated flankers may be similar. Therefore, the contrast threshold summation can be used to estimate the shape of the linear filters. In order to switch the facilitation to suppression Morgan and Dresp (1995) increased the ‘inducer’ contrast maximally but did not find the expected effect of suppression. Polat and Sagi (1993) briefly reported that at a test-flanker separation of 3λ, facilitation was evident when the flankers were at suprathreshold contrast. A recent study (Zenger and Sagi, 1996) tested this effect for a few target-flanker separations and for a wide range of flanker contrasts. Their results showed that facilitation occurred when the flankers were positioned at separations of 2λ or more and their contrast was 2–3 times above the target’s detection threshold. At separations of 3 and 4λ, the effect of flanker contrast on the magnitude of facilitation was negligible.

Here, we present new data to reinforce the notion that flanker contrast is not a critical parameter for long-range facilitation (Fig. 3A). The solid line (filled circles) denotes a typical lateral-masking function like those presented in Fig. 1. The effect of flanker contrast on the magnitude of the spatial interactions was tested. The dashed line (open circles) shows data when flanker contrast was about 2.5 times (20%) above the contrast threshold of the target. For this flanker contrast lateral interactions were measured between 0–4λ. Normal facilitation of about 0.3 log units was found at 3λ, but no effect was found for the other separations. Two further flanker contrasts were tested at 3λ: one was only slightly above the contrast threshold (10%, open triangle) and the other was a very high flanker contrast (75%, about 8 times above the contrast threshold, solid triangle). In spite of the large
Figure 3. (A) Effect of the flanker’s contrast on the lateral interactions. The response of one observer to the lateral interaction experiment, as described in Fig. 1. The flanker’s contrast was 40% (solid line, filled circles). The facilitation was found for 2 and 3λ. Response to the flanker’s contrast of 20% (about 2.5 times above the contrast threshold of the target; broken line, open circles). Facilitation effect of about 0.3 log units was still found. Two other flanker’s contrast; 10% (slightly above the target threshold, open triangle) and 75% (solid triangle) showed comparable facilitation. Thus the magnitude of facilitation at 3λ is not or only slightly dependent on the flanker’s contrast. Note also that at separations of less than 2λ, the 20% flanker’s contrast (broken line, open circles) didn’t suppress the target, indicating that the contrast was low enough not to suppress the target. (B) Response of individual neuron to Gabor patches, circular or elongated. The response to an individual Gabor patch that optimally fitted to the classical receptive field (CRF, left bar) was similarly facilitated when it was activated either by an elongated Gabor patch (2/1 aspect ratio) or with 2 Gabor flankers collinearly positioned outside the CRF. When the flankers were presented alone, outside the CRF, they failed to evoke a significant response from the neuron. This example supports the idea that elongated collinear facilitation may be due to non-linear facilitation between neurons and not from individual elongated linear CRF. The figure was modified from Polat et al. (1996).
Functional architecture

difference between flanker contrasts, the magnitude of facilitation was comparable. Note that a dramatic difference in the magnitude of suppression was found (open circles and solid circles). This differential effect strongly suggests that input inside and outside the CRF are qualitatively different mechanisms and that flanker contrast is not a critical parameter for long-range facilitation.

One can still argued that the available contrast range in this and other studies was simply not large enough and that, if there had been a way of increasing stimulation further (e.g. by current injection), suppression would have been observed. So, the fact that suppression was not observed does not conclusively rule out qualitative equivalence between the target and the flankers. However, in the experiment described above (Fig. 3A) we used a flanker contrast that was 8 times above the contrast threshold. This is relatively high contrast that usually suppressed the activity of neurons in the primary visual cortex (Polat et al., 1998a). The suppression effect can be also predicted from the ‘dipper function’, if the flankers are presented inside the linear filter, and their contrast is more than a few times above the contrast threshold (see Zener and Sagis, 1996). Therefore, considering that we used a contrast that was expected to evoke suppression (8 times above the threshold) we conclude that it is unlikely that the effect of facilitation is due to a summation of the target and flanker contrast from inside the linear filters.

Studies that used single-unit recordings from the cat area 17 (Polat et al., 1998a) further support the idea that the long-range interactions are not a summation of the flankers contrast by the CRF. The flankers facilitate the CRF only if there was weak activity inside the CRF (i.e. target + flankers, see Fig. 3B). An elongated target, twice than the optimal size of the CRF, facilitated the CRF by a magnitude similar to the Gabor flankers (Polat et al., 1996). However, when the flankers were positioned alone at distances of 3λ or more from the CRF, they failed to activate the CRF. This example shows that if the CRF is linearly elongated, then the flankers should activate the CRF from this distance, an effect that was not found. A similar effect has been shown in alert monkeys (Kapadia et al., 1995); facilitation was found only when line segments positioned inside and outside the CRF. Line segment alone outside the CRF did not elicit a significant response from the CRF. This is evidence of the non-linear stimulation of the CRF by the flankers. Without stimulation from inside the CRF, flankers alone have essentially no effect.

Consequently, the elongated collinear summation may be mediated by both the summation within each CRF (first stage, size of 2–3λ) and by interactions between CRF’s (second-stage) that preferentially connect them along a collinear axis. The recent results have clearly indicated that the visual cortex exhibits a preferential orientation pooling along the orientation axis over considerable distances in cortical space. Similarly-oriented first-stage filters are proposed to be collected, over space, into second-stage elongated filters (Morgan and Hotopf, 1989; Moulden, 1994; Polat et al., 1995; Levi and Waugh, 1996; Mussap and Levi, 1996; Polat and Norcia, 1996). Our approach is that lateral interactions form a second-order neural network
of excitation and inhibition regulating the response. A detailed description of this approach is follow.

FACILITATION

Psychophysical studies have shown that facilitation occurs when target and flankers are aligned (collinear) and separated by several wavelengths (cycles, \( \lambda \)) of the spatial frequency of the patches. Maximum facilitation occurs at separation of 2–3\( \lambda \) and progressively decreases up to a distance of 12\( \lambda \) (Polat and Sagi, 1993, 1994a, b). Recordings of visual evoked potentials show that the response to a target of low contrast is enhanced by collinear flankers up to 3 deg away (Polat and Norcia, 1996). Similar effects occurred in single-unit recordings from the primary visual cortex (Kapadia et al., 1995; Polat et al., 1998a), where collinearly arranged targets placed outside the CRF increased the firing rate of the neuron in the near-threshold region. Facilitation from a collinear configuration found only for low contrast of the target. In the VEP study (Polat and Norcia, 1996) maximal facilitation was found for 4% of contrast and reduced with increasing contrast reaching to no-effect at 16–32% of contrast. Some observers show inhibition at 32% of contrast. Neurons in the primary visual cortex show facilitation at low target contrast but the facilitation shifted to suppression at high contrast (Polat et al., 1998a). It has been shown that facilitation is more dominant near the contrast threshold and suppression at suprathreshold contrast.

SUPPRESSION

Suppression is a more general effect that can be categorized either by the spatial range (short or long), by the spatial configuration of the stimulus or by the contrast. Local suppression within an eccentricity of 2\( \lambda \) is found (Polat and Sagi, 1993, 1994a, b; Zenger and Sagi, 1996) and may result from a combination of mechanisms: contrast integration within the receptive field (Weber’s law) and broadband inhibition between neighboring cells (in space, orientation, and spatial frequency). As a function of spatial configuration, suppression is found for collinear configurations (Kapadia et al., 1995; Polat et al., 1998b), iso-orientations (Cannon and Fullenkamp, 1991; Grinvald et al., 1994; Levitt and Lund, 1997; Sengpiel et al., 1998), non-collinear configurations (Grinvald et al., 1994; Silito et al., 1995; Levitt and Lund, 1997; Polat et al., 1998b; Sengpiel et al., 1998), and textures (Knierim and Van Essen, 1992; Kapadia et al., 1995). As a function of contrast, suppression from collinear flankers is dominant at suprathreshold contrast (Polat et al., 1998a) but non-collinear configurations can suppress the target for a wide range of contrast (Grinvald et al., 1994; Polat and Norcia, 1996; Wilkinson et al., 1997; Polat et al., 1998a; Sengpiel et al., 1998).
FUNCTIONAL SIGNIFICANCE

Facilitative and suppressive center-surround interactions may be organized differently to subserve different functional rules. Facilitative interactions may be organized mainly along the neuron’s optimal orientation forming a collinear integration field that may underlie the detection of extended contours (Polat and Sagi, 1993, 1994a, b; Kapadia et al., 1995; Polat and Norcia, 1996; Polat et al., 1998b).

Suppression is a more general phenomenon that is found for many center-surround combinations of spatial configurations, orientations and spatial separations. We suggest that suppression may have different functions depending on the contextual parameters. Suppression for non-collinear configurations may act as a contrast gain control (Heeger, 1992; Sengpiel et al., 1998, rightward shift of the contrast response function) to increase differential sensitivities between neighboring regions. This effect may serve to enhance surface perception, pop out and discontinuities. However, collinear suppression at suprathreshold contrasts acts to attenuate the responses of highly active neurons. In conjunction with the collinear facilitation (near contrast threshold) suppression may serve to increase the response similarity between neurons belonging to the same contour. Thus, increasing and decreasing the firing rate may decrease their response variability (since the response variance is proportional to the mean response, and the mean response is more similar; see below Response similarity), an effect that can be used in grouping of neurons coding the same contour. The idea of response similarity will be emphasized later in this article (see Response similarity below).

NEURAL NETWORK

The facilitation and suppression of contrast response thresholds by the lateral interactions show that regulation of the contrast gain of local filters is context dependent. Our model of lateral interactions is presented in Fig. 4A. This is based on the assumption that excitation and inhibition produce a network of neuronal connectivity that modifies the neuronal response. In this model, each filter receives three types of visual input: direct thalamic-cortical excitatory input, lateral excitation, and lateral inhibition. The excitation is organized along the filters optimal orientation (vertical lines in the elliptical patch) and is superimposed on a suppressive area (dotted area) surrounding the filters. The balance of the network may control the contrast response function of the individual filter. The row of Gabor patches demonstrates how local oriented filters aligned along their optimal orientation might produce an elongated collinear filter (Polat and Norcia, 1998; Polat and Tyler, 1999). Similar computational neural network models of lateral interactions have been suggested (Wilson and Cowan, 1973; Stemmler et al., 1995; Adini et al., 1997; Yen and Finkel, 1998). Note that the network may also be influenced by top down interactions.

We want to emphasize two important effects throughout the rest of the manuscript (i) the inputs from the lateral interactions summate non-linearly to the CRF's
Figure 4. (A) A neuronal network model for lateral interactions. The target receives three types of visual input: direct thalamic-cortical excitatory input, lateral excitation and lateral inhibition. The excitation is organized along the filters optimal orientation (vertical lines in the elliptical patch) and superimposed on a suppressive area (dotted area) surrounding the filters. The balance of the network may control the contrast response function of the individual filter. The row of Gabor patches demonstrates how local oriented filters aligned along their optimal orientation may produce an elongated collinear filter (Polat and Norcia, 1998; Polat and Tyler, 1999). (B) The specificity of facilitation for collinear configuration. facilitation was found when the observer was tested with a collinear configuration (left bar) and slight facilitation was found for a side-by-side configuration (middle bar), but the facilitation disappeared when both configurations were combined. See text for explanation of this effect.

output and (ii) the interactions between neurons aligned along the optimal neuronal orientation (collinear) are distinct from the other interactions.

The specificity of the facilitation for collinear contours and the non-linearity of the interactions are shown in Fig. 4B. Here we present new psychophysical data of contrast detection of a Gabor target. The y-axis shows the amount of target facilitation. The left bar show a typical target’s facilitation evoked by collinear flankers in consistent with earlier studies (Polat and Sagi, 1993, 1994a, b). The facilitation is reduced when the same Gabor flankers are placed laterally (i.e. side-by-side, middle bar), consistent with the results presented by Polat and Sagi (1994a). The amount of facilitation from iso-oriented Gabor patches positioned side-by-side was smaller and found only from a short range (Polat and Sagi, 1994a). This facilitation from the suppressive surround (in the model) is explained as a dis-inhibition effect (Polat and Sagi, 1993, 1994a; Adini et al., 1998). When both configurations, collinear and side-by-side, were combined (right bar), the facilitation disappeared. The lack of the facilitatory effect show that the excitatory and inhibitory processes are integrating non-linearly in the network. This effect might be explained either due to suppression between the high-contrast flankers (side-by-side and collinear), thus preventing the flankers facilitating the target, or by non-linear integration of facilitation and suppression by the target. Taken together, this experiment shows that existence of collinear interactions may not be sufficient or effective when the visual stimulus does not form a contour.
CONTOUR INTEGRATION

Collinear facilitatory interactions are believed to subserve major grouping tasks such as contour integration. The local rules of interactions that govern our ability to link contour segments together have been studied in a contour detection paradigm (Field et al., 1993; Kovács and Julesz, 1993; Pettet et al., 1998), where observers have to find a continuous path of Gabor signals embedded in noise. The chains of Gabor elements are easily seen at certain inter-element spacings (proximity) and small orientation differences (smoothness) between the elements comprising the path and closed smooth shapes of contours (closure) — effects that seem to obey the Gestalt rules and are reminiscent of the rules found for collinear facilitation. It has been suggested that contour integration may rely on the long-range interactions described above (Kovács and Julesz, 1993; Polat and Sagi, 1994a, b; Kovács et al., 1996; Polat et al., 1996; Polat and Norcia, 1996; Pettet et al., 1998; Yen and Finkel, 1998).

Figure 5 shows how collinear interactions can mediate contour integration. Collinear configurations may be detected by elongated collinear filters to produce a collinear interaction field (Fig. 5A). Since collinear interactions can tolerate small deviations from perfect alignment (Polat and Sagi, 1993, 1994a; Field et al., 1993; Kovács and Julesz, 1993; Pettet et al., 1998), a chain of collinear filters can produce a field of smooth contour (Fig. 5B, C). Thus orientation differences between the Gabor elements as much as 90 deg can be grouped when they belong to the same contour and are connected with Gabor elements in intermediate orientations (Fig. 5B, C). Therefore, interactions between ‘far’ orientations are made possible by a chain of ‘near’ connections (smoothness) between intermediate orientations. This effect is reminiscent of the effect when very long interactions were established via a chain of local intermediate filters (Polat and Sagi, 1994b).

In a recent study we have shown that a critical factor in contour detection is the relative ratio between the background elements and the target elements (Kovács et al., 1996). Increasing the density of background elements (increasing their number) increases the detection threshold (masking effect), thus setting a detection threshold that is determined by the background-to-target elements’ density ratio. These types of experiments suggest that the background elements contribute a certain amount of ‘noise’ that sets a limit to contour detection.

RESPONSE SIMILARITY

As described above, the contrast response function of neurons evoked by elements belonging to a contour is different than the contrast response function of neurons evoked by element belonging to randomly oriented elements. The dynamic response range (DRR) of the neuron (with no context), from contrast threshold up to saturation, is about 2 and 2.8 log units (Polat et al., 1998a, Fig. 2). The DRR of the same neuron under collinear interactions is 0.47 and 0.6 log units. Similar
Figure 5. Formation of elongated collinear fields of interactions. (A) Elongated filters pooling collinear textures to form a long collinear field of interactions. (B) Since facilitation can be found for configurations that are slightly different from collinear configurations, elongated filters can pool the outputs from a few textures that form an almost collinear configuration. A combination of collinear elongated filters can form a curved smooth interaction field. (C) Contour like that shown in (B) but now embedded within a randomly oriented background of Gabor elements. Observers can see such a contour effortlessly.

effects have been shown for neurons under iso-orientation modulations (Sengpiel et al., 1998). Thus the DRR of neuron responding to a contour is only about 1/5 (20%) of the maximal DRR of the neuron when it is responding to high contrast non-collinear background elements (the DRR under cross-orientation suppression
remains unchanged and is rightward shift of the contrast response function; Sengpiel et al., 1998). Note that on average the difference response between neurons responding to the same contour is only $\pm 0.23 - 0.3$ log units or only $\pm 10\%$ of the maximal DRR. Thus, the responses of neurons responding to a contour are relatively similar to one another.

The response of individual neurons in the visual cortex is highly variable (noisy). A nearly constant ratio between the mean response and the mean variance is found under a variety of experimental conditions, and throughout the visual pathways, implying that this is an innate property of these neurons (Tolhurst et al., 1983; Geisler and Albrecht, 1995). Therefore, since the DRR of neurons responding to the contour is smaller than the DRR of neurons responding to the background, it is clear that the response variance of the neurons responding to contour elements is much smaller than that of neurons responding to the background elements. Thus a contour of ‘similar responses’ will be formed. In this way, neurons may ‘translate’ grouping principles of similarity of the retinal image in to similarity in the neuronal code. Note also that according to this approach, introducing contrast jitter between the contour elements, will not diminish contour detection (Hess et al., 1998).

THE ANATOMICAL BASIS OF THE LONG-RANGE INTERACTIONS

The anatomical basis of the long-range interactions may rely on the long-range connections (Gilbert and Wiesel, 1985, 1989; Bolz and Gilbert, 1989; Grinvald et al., 1994; Ts’o et al., 1986) that occur between similar-orientation columns (Malach et al., 1993; Weliky and Katz, 1994; Kivvarday et al., 1996). These connections span large distances and can convey contextual information (Gilbert and Wiesel, 1983; Fitzpatrick, 1996; Schmidt et al., 1997). For a recent review see Callaway (1998). Moreover, the pattern of anatomical connections is elongated and tends to interconnect iso-oriented columns that correspond to collinear stimuli in the visual cortex of tree shrews (Fitzpatrick, 1996) and cats (Schmidt et al., 1997). Thus, specificity in the spatial arrangement of local circuit axon arbors appears to be important for shaping the response properties of neurons in the visual cortex (Fitzpatrick, 1996). For a review of the role of long-range interactions in grouping see Spillmann and Werner (1996).

SYNCHRONIZATION AS A PARALLEL EFFECT TO THE COLLINEAR INTERACTIONS

Numerous studies have shown that neurons can synchronize their discharges with a precision in the millisecond range (Lowel and Singer, 1992; for review see Singer and Gray, 1995). This synchronization was found between spatially separated neurons and requires stimulus configurations that resemble those described for collinear interactions. It has been suggested that synchronization may underlie
grouping (Singer and Gray, 1995). In the visual cortex of humans, using VEP recording technique, Polat and Norcia (1996) found that the facilitation of a low contrast Gabor target by collinear flankers involved a phase lead of the response, pointing to the possibility that both the response amplitude and the temporal response are modifiable by the long-range interactions. A recent theoretical model (Yen and Finkel, 1998) has suggested that strongly facilitated cells undergo temporal synchronization and that perceptual salience is determined by the level of synchronization. This model postulates that contour detection is dependent on simple neuronal network rules of collinear facilitation and surround inhibition, similar to those shown in Figs 2A and 5.

AMBYLOPIA AS A FAILURE OF LATERAL INTERACTIONS

Amblyopia is a monocular disorder of spatial vision caused by abnormal binocular input during a critical period of development. Amblyopic observers may suffer from reduced visual acuity, reduced sensitivity for spatial contrast (Gstaldner and Green, 1971; Levi and Harwerth, 1977; Bradley and Freeman, 1981), reduced vernier acuity (Bradley and Freeman, 1981; Levi and Klein, 1982), spatial distortion (Hess et al., 1978; Bedell and Flom, 1981, 1983; Lagraze and Sireteanu, 1991), abnormal spatial interactions (Polat et al., 1997) and impaired contour detection (Kovács et al., 1996; Hess et al., 1997).

Abnormal contrast sensitivity functions (CSF) occur in most amblyopic eyes, and mainly at high spatial frequencies, with little or no loss of contrast sensitivity at low spatial frequencies (Gstaldner and Green, 1971; Levi and Harwerth, 1977). In other words, the contrast threshold in amblyopic eyes is usually higher than that of the normal eyes probably due to a weak signal or increased intrinsic noise. Note that this effect may reduce the S/N ratio in the amblyopic eye. Thus amblyopes may have abnormally high degrees of intrinsic noise, which may form the basis of their abnormal CSF (Levi and Klein, 1990). For a detailed review see Levi (1991).

Abnormal spatial interactions were recently observed in amblyopic observers (Mussap and Levi, 1995; Polat et al., 1997). In psychophysical and VEP experiments, amblyopes exhibited several deviations from normal patterns. Their facilitation for collinear configurations was either markedly lower than normal or was replaced by inhibition (Polat et al., 1997). This loss of normal spatial facilitation may contribute to the grouping deficit usually present in amblyopia. This abnormality in spatial interaction could underlie the elevated contrast threshold usually present in amblyopia, and which is assumed to underlie the reduced positional acuity of amblyopic eyes. Furthermore, neurons in the visual cortex of cats that were reared under conditions in which they developed amblyopia showed abnormal lateral interactions (Kasamatsu et al., 1998) and a lack of synchronization between neurons (Roelfsema et al., 1994) that can possibly be mediated by the lateral interactions (Lowel and Singer, 1992). Thus abnormal synchronization in amblyopic
cats may indicate that the long-range interactions were abnormal, further supporting our proposal that the lateral interactions in amblyopia are abnormal.

More recently it has been shown that amblyopic observers failed in the task of contour integration (Kovács et al., 1996). The results show a remarkable deficit in the amblyopic eye as compared to the fellow eye of amblyopic observers, and to the performance of normal subjects. The amblyopic subjects could not group globally defined contours together, which may be due to their loss of long-range connectivity between spatial filters. These results indicate the possibility of more severe abnormalities of spatial integration in amblyopic eyes and support the suggestion that there is a connection between impaired lateral interactions and contour grouping in amblyopia. A similar failure of contour detection was found in strabismic (Hess et al., 1997) but not in anisometropic (Hess and Demanins, 1998) amblyopes.

PLASTICITY OF LONG-RANGE INTERACTIONS

When observers perform a visual (or any other sensory) discrimination task, their performance often improves with practice, even with simple tasks. During the last decade, perceptual learning was shown to occur in a variety of visual tasks (for a review see Sagi and Tanne, 1994). Using a lateral masking paradigm, it has been found that perceptual learning involves an increased range of interactions in early vision (Polat and Sagi, 1994b). In these studies, observers were trained to detect a Gabor signal in the presence of two high-contrast flankers. Practice caused a continuous increase in the range of interactions, in that long-range interaction could not be established before medium-range interactions became effective. Long-range interactions were suggested to be produced by chains of local interactions. Moreover, this learning effect was context-dependent, i.e. it only occurred when the observers were trained with the target and flankers positioned in a collinear configuration, but not when the same target and flankers were positioned in a non-collinear configuration (Polat and Sagi, 1994b, 1995).

An extended contrast summation up to 12λ in the elongated collinear configuration was found for one observer (observer UP, Polat and Tyler, 1999; see also Fig. 3). This observer had under gone extensive practice in a wide variety of previous lateral interaction experiments, and detection of elongated Gabor patches. Therefore, his extended summation may have been due to improvements of collinear long-range facilitation like those described in Polat and Sagi (1994b). This type of practice effect supports the notion that very long-range interaction can be formed from a chain of smaller filters connected collinearly. These long-range interactions between filters arranged collinearly may underlie the extended contrast threshold summation found for this observer.
PLASTICITY IN AMBYOPIA

Plasticity in adults with ambyopia has recently been observed (Levi and Polat, 1996; Levi et al., 1997). Repetitive practice led to a substantial improvement in the vernier acuity in the amblyopic eyes of adults with naturally occurring amblyopia. In some of the observers, the improvement in vernier acuity was accompanied by a commensurate improvement in Snellen acuity up to normal vision. This improvement in Snellen acuity is consistent with the close connection between vernier and Snellen acuity noted earlier (Levi and Klein, 1982). This result is surprising, because the physiological effects of strabismus or lid suture on the cortex are generally thought to be irreversible after a critical period (typically 3–4 months in cats and monkeys; Levey et al., 1980; Boothe et al., 1985; and only a few years in children).

SUMMARY

The recent results obtained from human observers and individual neurons have suggested that normal lateral interactions produce a neuronal network that is formed by excitatory and inhibitory inputs. Each neuron receives three types of visual input: direct thalamic-cortical excitatory input, lateral excitation, and lateral inhibition. The excitation is organized along the filters’ optimal orientation and is embedded in inhibitory connections surrounding the filter. The balance of the network may control the contrast response function of the individual filter. Under specific conditions, the visual cortex exhibits preferential interactions along the orientation axis over considerable distances in cortical space. Thus, iso-oriented first-stage filters are thought to be collected, over space, into a second-stage elongated collinear field. The collinear interactions may increase the response similarity between the neurons thus enhancing contour integration.

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REFERENCES


Kovács, I. and Julesz, B. (1993). A closed curve is much more than an incomplete one: effect of closure in figure-ground segmentation, Proceedings of the National Academy of Sciences USA 90, 7495–7497.


