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Associative learning in early vision

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Abstract

Sensory discriminations often improve with practice (perceptual learning). Recent results show that practice does not necessarily lead to the best possible performance on the task. It was shown that learning a task (contrast discrimination) that has already reached saturation could be enabled by a contextual change in the stimulus (the addition of surrounding flankers) during practice. Psychophysical results with varying context show a behavior that is described by a network of local visual processors with horizontal recurrent interactions. We describe a mathematical learning rule for the modification of cortical synapses that is inspired by the experimental results and apply it to recurrent cortical networks that respond to external stimuli. The model predicts that repeated presentation of the same stimulus leads to saturation of synaptic modification, such that the strengths of recurrent connections depend on the configuration of the stimulus but not on its amplitude. When a new stimulus is introduced, the modification is rekindled until a new equilibrium is reached. This effect may explain the saturation of perceptual learning when practicing a certain task repeatedly. We present simulations of contrast discrimination in a simplified model of a cortical column in the primary visual cortex and show that performance of the model is reminiscent of context-dependent perceptual learning. © 2004 Elsevier Ltd. All rights reserved.

Keywords: Contrast discrimination; Perceptual learning; Context-enabled learning; Spike-time-dependent synaptic plasticity

1. Introduction

Performance on a variety of visual tasks improves with practice. The phenomenon extends to simple tasks, such as orientation discrimination, Vernier acuity and texture discrimination. Learning was found to be specific to basic image features, such as orientation, spatial-frequency (Fiorentini & Berardi, 1981), target location and eye of stimulation (Karni & Sagi, 1991). The high feature-specificity of learning was taken to predict that learning takes place at relatively low-level cortical areas (Fahle, Edelman, & Poggio, 1995; Fiorentini & Berardi, 1981; Karni & Sagi, 1991). The task-dependency of learning was taken to indicate that learning is controlled (gated) by high-level cortical areas (Ahissar & Hochstein, 1993; Karni & Sagi, 1995). Evidence that points to neural correlates of perceptual learning in the primary visual cortex of the monkey was recently obtained (Gilbert, Sigman, & Crist, 2001). There are a few reports of studies combining perceptual learning methods and VEP recordings in humans. A spatio-temporal activation pattern with steep

gradients over the primary visual cortex appears to be correlated with plasticity in the human visual system (Skrandies & Fahle, 1994; Skrandies, Lang, & Jedynek, 1996). Some perceptual learning effects persist through life time without further practice. In the case of texture discrimination the performance improvement obtained within a few days (5–10) was preserved after 3 years (Karni & Sagi, 1993). Overall, the experimental results accumulated during the last decade support the view that sensory regions in the adult cortex, including the primary visual cortex, are modifiable through the whole life span (Karni & Bertini, 1997; Sagi & Tanne, 1994). Massive functional remapping seems to take place within the visual cortex of humans when the input from a region of the visual field is disrupted due to scotoma (Casco, Campana, Grieco, Musetti, & Perrone, 2003). More surprisingly, recent evidence show that the primary visual cortex of the congenitally blind is activated in verbal memory tasks (Amedi, Raz, Pianka, Malach, & Zohary, 2003). Perceptual learning was shown to improve vision in humans with amblyopia, a developmental disorder, thus supporting the view that at least some perceptual learning effects reflect an extension into adulthood of the developmental critical

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period that was thought to be limited to young age (Polat, Ma-Naim, Belkin, & Sagi, 2004).

The phenomenology of perceptual learning is rich and diverse, pointing to a multiplicity of underlying mechanisms. Considering that perceptual tasks can be of different type (detection, discrimination, recognition) and are applied on stimuli of different complexities (light, texture, patterns), one expects the learning mechanisms to differ accordingly. Indeed, the expectation to find the same phenomenology for all learning tasks used in vision can yield only frustration (Chung, Legge, & Cheung, 2004). Not surprisingly, theoretical accounts of perceptual learning fail to capture the diversity of the learning types observed. In particular, the processing level that is modified during learning was considered. A prevailing theory of perceptual learning assumes that the observer merely learns to better discriminate different ‘perceptions’ (Gibson, 1969) (i.e. patterns of activity in the low-level network) and learns to optimize his/her decision strategies, while the low-level sensory network that responds to the stimulus (such as a line segment or texture) is left untouched. Recent evidence points to the possibility that perceptual learning reflects plasticity at an intermediate level of weighting inputs to decision (Doshier & Lu, 1998, 1999). Doshier and Lu (1998) had subjects practicing an orientation discrimination task with the target embedded in a noise pattern. Their results point to the possibility that learning involves external noise exclusion and internal noise reduction via modification of weights between low-level processors and the decision stage. Schubo, Schlaghecken, and Meinecke, (2001) suggest that learning in texture segmentation consists of, though not limited to, separating the task-relevant signal (texture) from the task-irrelevant signal (mask). In general, all learning phenomena may involve a variety of functionalities. Learning of a texture segmentation task, a task considered to be ‘effortless’ (Julesz, 1965, 1981) and to be limited by low-level visual mechanisms (Rubenstein & Sagi, 1990), was shown to involve both ‘high-level’ (binocular) and ‘low-level’ (monocular) processes (Karni & Sagi, 1993).

The work described here presents an attempt to explain the improvement in performance by assuming specific modifications in the low-level network. These changes are modeled using learning rules that depend on the network activity only, preferably on the activity in the connected units (local rules), and not on variables external to the network (e.g. stimulus and task, though both may affect network activity). For example, based on a model of texture discrimination (Rubenstein & Sagi, 1990), it is possible to explain texture learning by an increase in the strength of the lateral-inhibitory connections between units responding to the local elements comprising the texture and/or by an increase of the efficacy of excitatory interactions across the texture boundary that separates foreground from background. The latter method is expected to increase the saliency of the target embedded in the given background while the former to reduce the background activity—both

leading to improved performance in accordance with the constraints imposed by the experimental data (Karni & Sagi, 1991). Polat and Sagi (1993, 1994a) studied the lateral interactions that are hypothesized to underlie texture discrimination and perceptual grouping, by examining the effect of spatial context (Gabor flankers) on the contrast detection threshold of a localized target (Gabor signal). The results showed a pattern of lateral interactions with short-range inhibition and long-range excitation. These spatial interactions had a pattern similar to that observed in the monkey and the cat primary visual cortex (Bosking, Zhang, Schofield, & Fitzpatrick, 1997; Kapadia, Westheimer, & Gilbert, 2000; Lowel & Singer, 1992; Malach, Amir, Harel, & Grinvald, 1993; Schmidt, Goebel, Lowel, & Singer, 1997), with strongest interactions for co-oriented and co-aligned stimuli (Polat & Sagi, 1994a). Observers that practiced the contrast detection task in the presence of flankers showed after training either no-change, increase or decrease in interaction range, depending on the pattern of stimulation (Polat & Sagi, 1994b). It was suggested (Polat & Sagi, 1994b) that the stimuli activate specific nodes in a network with specific lateral interactions where the learning is governed by a combination of Hebbian and anti-Hebbian rules (Hebb, 1949) between the connected nodes. It seems that, during practice with visual stimuli, the early vision network is modified in a way that reflects the correlations between the stimuli encountered during task performance, thus recording accumulated associations between those stimuli that are of interest to the system (as defined by its connectivity) rather than merely improving the information processing required for the task. It follows that we are not able to learn spatial configurations that do not match the connectivity of the visual system. Obviously, some additional selection process that is based on stimulus relevance is required to prevent changes in the low level network due to accidental correlations. It was suggested that perceptual learning operates only on task related stimuli in a task-specific manner (Ahissar & Hochstein, 1993). Recent results, however, show that improvement on a foveal visual task involves also improvement on an unrelated task that is performed on peripheral stimuli that were unattended during learning (Seitz & Watanabe, 2003). In these experiments different peripheral stimuli were paired with foveal targets and non-target, thus it was possible to isolate learning effects that were paired with foveal-targets presentation. It is possible that the task-driven gating process that controls learning reinforces synaptic changes on a much larger network than required for an efficient processing of the experimental task, thus enabling learning of unattended stimuli that are coupled with the task relevant stimuli.

We consider here in detail the basic task of contrast discrimination. The task is peculiar in the context of perceptual learning as it shows stable performance when repeated many times. Thus, in this case, practice does not ‘make perfect’. In fact, the only observable effect after more than 40 sessions of practice was a slight deterioration in

performance (Dorais & Sagi, 1997; Zenger & Sagi, 2002), indicating that this basic task might have reached its optimal performance during normal development, or within the time frame of fast learning processes operating during the first test session (Karni & Sagi, 1993). Later it became evident that this was not the case, as new experiments showed improved contrast discrimination thresholds after training with targets that were embedded in a spatial context (Adini, Sagi, & Tsodyks, 2002). This effect was called ‘context-enabled learning’. Adini et al. (2002) attributed this learning effect to changes in the low-level neuronal network, triggered by additional inputs provided by lateral interactions. Based on a neural network model of contrast discrimination, it was suggested that context-enabled learning is mediated by a recently suggested synaptic learning rule that combines both increase and decrease in synaptic efficacy depending on the activity level of pre- and post-synaptic neurons (Senn, Markram, & Tsodyks, 2001). The experimental evidence leading to this conclusion will be described next, followed by a theoretical exposition.

The human contrast response function describes the dependence of contrast discrimination thresholds on contrast (TvC: Threshold vs Contrast). The function exhibits a well-known characteristic non-monotonic behavior, as shown in Fig. 1, with a ‘dipper’ typically obtained at around the contrast detection threshold value. At higher base contrasts, thresholds increase continuously with base contrast, a phenomenon which is a reminiscent of Weber’s Law (though better described by a power dependency). The TvC function has been used to predict the internal response

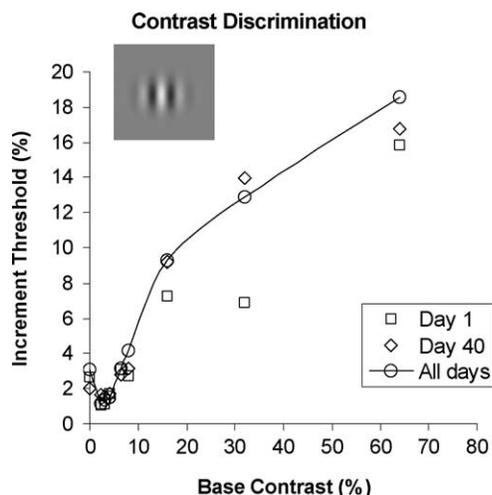


Fig. 1. Contrast discrimination thresholds as a function of base contrast: A typical TvC curve (Threshold vs Contrast). Data for a single observer (OY) are shown, using a Gabor signal as stimulus (see inset). The open circles represent averages of 80 measurements each, collected in 40 daily sessions. Separately shown are also data from the first day (\square) and from the last day (\diamond), demonstrating the absence of improvement with practice on the task. This result implies a fixed transformation from stimulus contrast to internal response, with maximal sensitivity (gain) achieved with base stimuli at around detection threshold ($\sim 3\%$). The internal response function can be derived by integrating the shown discrimination curve (Fechner, 1860).

to contrast within the visual system. The most popular model is the ‘non-linear transducer function’ (Legge, 1981; Legge & Foley, 1980; Wilson, 1980), which assumes that changes in discrimination thresholds can be attributed to changes of gain (slope) in the transducer function (a function that transforms contrast to internal response) and thus predicts that thresholds are inversely proportional to the slope of the transducer function (following Fechner (1860)). Performance on contrast discrimination tasks has been found to be stable across repetitions. Dorais and Sagi (1997) measured TvC functions for Gabor signals for many days from the same observers and did not find any improvement with practice (see also Zenger and Sagi (2002)). A new example is depicted in Fig. 1, where observer OY practiced the contrast discrimination task for 40 daily sessions without any improvement. This is in contrast with the many learning effects described above and in particular with the effects observed in similar contrast masking tasks, with the only difference between the stimuli being the orientation offset between the target (increment) and the maskers (Dorais & Sagi, 1997). However, the orientation-masking task should be viewed as a pattern discrimination task and not as contrast discrimination task where the overall contrast of the target need to be judged. We also make here a distinction between contrast discrimination tasks that are practiced with stimuli having a large range of contrasts and tasks that involve only a single contrast. The latter can be viewed as a specific case of pattern discrimination and may improve with practice (Sagi, Adini, Tsodyks, & Wilkonsky, 2003; Yu, Levi, & Klein, 2003).

2. Effects of lateral interactions on contrast discrimination

When *contrast discrimination* is performed in the presence of two flanking stimuli, discrimination thresholds generally increase with respect to the no-flank condition (Adini & Sagi, 2001; Bonneh & Sagi, 1999b; Chen & Tyler, 2001; Zenger, Braun, & Koch, 2000; Zenger-Landolt & Koch, 2001). The details of this masking effect depend on flankers contrast, on the distance between target and flankers, on stimulus configuration (collinear or parallel) and on the location of the stimulus in the visual field (fovea or periphery). Of particular significance is the contrast dependency of the lateral masking effect. For very low target contrasts, the flankers improve thresholds (as in Polat and Sagi (1993)), but this effect is reversed once the target base is increased to above detection threshold (Fig. 3). This result is explained by assuming inhibitory processes that dominate the high contrast regime and excitatory processes at low contrast (Stemmler, Usher, & Niebur, 1995; Usher, Bonneh, Sagi, & Herrmann, 1999). Results recorded from the cat visual cortex (Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998) support such a contrast dependency of lateral interactions. Psychophysical evidence pointing to

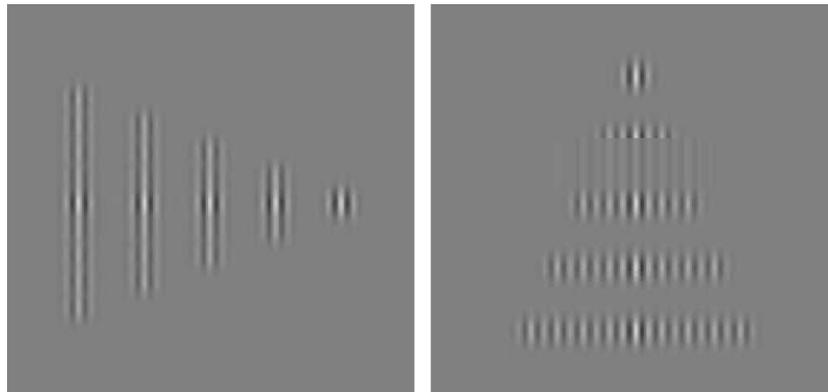


Fig. 2. Stimuli used to probe lateral interactions. Each stimulus consists of one chain of Gabor signals of variable length ($N = 1-9$ shown, 2λ separation). In the experiments, observers' task is to detect a contrast increment at stimulus center.

contrast-dependent lateral-interactions is shown in Fig. 3. Fig. 3 shows data from experiments where the number of flankers was varied (as in Fig. 2), designed to probe mutual interactions between flankers through their effect on the flanked target. The main result from this type of experiments is the cancellation of the lateral facilitation produced by two flankers (Adini & Sagi, 2001; Adini, Sagi, & Tsodyks, 1997; Polat, 1999; Solomon & Morgan, 2000). To test the contrast dependency of these effects, contrast discrimination was tested with different base contrasts (0.9, 1.1 and 6 times detection thresholds), yielding discrimination thresholds similar to those presented in Fig. 1, shown in Fig. 3 at chain length of $N = 1$. Increasing the number of flankers did not affect the discrimination thresholds when flankers were just below threshold (by 10%), while it significantly reduced the facilitation when flankers were just below threshold (by 10%). The most interesting aspect of the data is the oscillatory pattern that emerged with above threshold

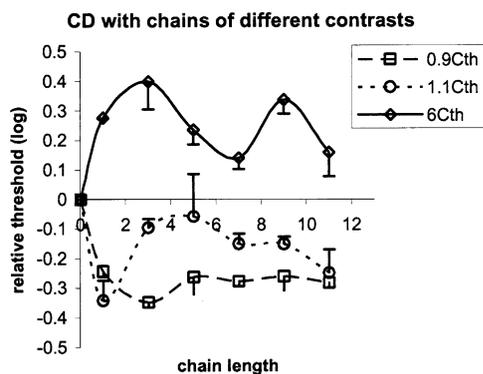


Fig. 3. Contrast discrimination (CD) thresholds as a function of chain length, relative to contrast detection threshold (chain length, $N = 0$). With $N = 1$, the task is equivalent to a contrast discrimination task, as shown in Fig. 1, with the different curves showing data for base contrast of 0.9, 1.1 and 6 times the detection threshold. For $N > 1$, the target is flanked by $(N - 1)/2$ Gabor signals on each side, with their contrast equal to the base contrast. The main effect to note is that the base contrast effect is cancelled by increasing chain length with chain contrast above threshold, pointing to lateral inhibitory interactions. (Each datum point is the average of 2 observers, with error bars showing 1 SEM). Results for the two higher contrast levels are from Adini and Sagi (2001).

chains, pointing to strong lateral-inhibitory interactions between the local units that respond to the flankers. These interactions are of short range as increasing the separation between the flankers from 2λ to 3λ (λ being the Gabor wavelength) eliminated the inhibitory effects (Fig. 4). The oscillatory behavior of contrast discrimination points to horizontal feedback interactions within the visual system (Adini et al., 1997) rather than to feed-forward processing or feedback from higher processing levels (Bair, Cavanaugh, & Movshon, 2003).

3. Effects of lateral interactions on contrast discrimination learning

The contrast discrimination curve does not change with practice (Fig. 1). This is in contrast with the many other visual tasks reported to improve after training. Included in this list are basic tasks such as orientation

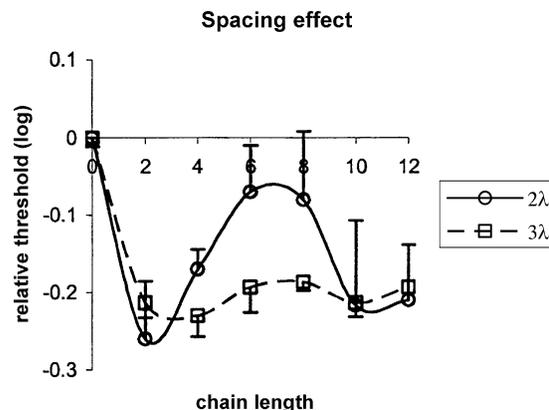


Fig. 4. Effect of spacing between flankers on lateral interactions. Here a contrast detection task was used in the absence of flankers ($N = 0$) and in the presence of high contrast flankers ($C = 30\%$). The addition of two flankers, one on each side, facilitated performance (as in Polat and Sagi (1993)) at both distances tested (2 and 3λ). Increasing chain length resulted in a cancellation of the facilitation with 2λ spacing but not with 3λ spacing, pointing to short-range inhibitory interactions (each datum point represent average from 3 observers, with error bars showing 1 SEM).

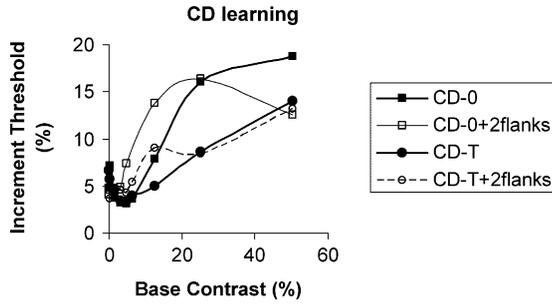


Fig. 5. Effects of practicing contrast discrimination with flankers (Figure 2) on the contrast discrimination curve. Data are shown for contrast discrimination without flankers, before (■) and after (●) practice with flankers. The performance in the presence of 2 flankers (one on each side) is shown by the corresponding open symbols (□,○). The main effect to note is the improved discrimination performance (continuous lines, average of 3 observers from Adini et al. (2002)).

‘pop-out’ (Ahissar & Hochstein, 1993; Karni & Sagi, 1991), spatial-frequency discrimination (Fiorentini & Berardi, 1981), spatial acuity (Fahle & Edelman, 1993; Fahle et al., 1995), motion detection (Ball & Sekuler, 1987), all of which are assumed to involve at least some plasticity at early stages of visual processing. Some studies show improved contrast detection (Mayer, 1983; Sowden, Rose, & Davies, 2002) and discrimination (Yu et al., 2003) for individual contrast levels, when only a single contrast level is practiced. These effects are very specific to contrast (Yu et al., 2003) and depend on the observer having exact knowledge of the targets’ contrast (Sagi et al., 2003). Recently, we have shown that contrast discrimination thresholds can be improved as a result of practicing the task with the target stimulus flanked by similar stimuli, as shown in Fig. 2 (Adini et al., 2002). After training with chains of flankers (see Methods), discrimination thresholds improved for both conditions, with chains and without chains, as shown in Fig. 5. This phenomenon, termed ‘context-enabled learning’, is the target for the model described in Section 4.

4. Model

Here we present a model that attempts to relate the psychophysical effects described above to synaptic plasticity in the primary visual areas. Our basic assumption is that the CD performance is mediated by the activation of an interconnected local neural networks (Foley, 1994; Wilson & Humanski, 1993), with synaptic connections that are modified in an activity-dependent manner. The main challenge for the model is to explain why the performances are stable after repeated activation of the network with the same stimulus of different contrasts, but improve after practicing the task with a changed stimulus configuration. This observation indicates that repeatedly activating the network with the same visual stimulus should lead to certain equilibrium values for the strengths of synaptic connections,

that should be sensitive to the configuration but not to the amplitude of the stimulus. In order to achieve this behavior in the model, we use a particular rule for long-term changes in synaptic strength (Senn et al., 2001), that was formulated while studying the implications of spike-time-dependent synaptic plasticity (Bell, Han, Sugawara, & Grant, 1997; Bi & Poo, 1998; Markram, Lubke, Frotscher, & Sakmann, 1997). The rule relates the change in the probability of neurotransmitter release (P_r) to the instantaneous pre- and post-synaptic firing frequencies (f_{pre} and f_{post}) in a way that combines Hebbian (up-regulation) and anti-Hebbian (down-regulation) terms:

$$\frac{dP_r}{dt} = r_u(P_r f_{pre})(f_{post}^2) - r_d(P_r f_{pre})^2 f_{post} \quad (1)$$

The peculiar properties of this proposed learning rule can be seen if we rewrite Eq. (1) in a slightly different way:

$$\frac{dP_r}{dt} = r_u P_r f_{pre} f_{post} (f_{post} - \varepsilon P_r f_{pre}), \quad (2)$$

where ε stands for r_d/r_u . According to this equation, when the pre- and post-synaptic are firing with stationary rates, synaptic connection between them reaches a steady value of

$$P_r = \frac{f_{post}}{\varepsilon f_{pre}} \quad (3)$$

Thereafter, the release probability will remain steady as long as the ratio between the post- and pre-synaptic rates remains constant. When the rates deviate from this constant ratio relationship, the synaptic change will resume until the new equilibrium point is reached. In other words, the release probability of the connection serves as a memory trace for the ratio between the pre- and post-synaptic rates experienced in the past.

We now turn to our simplified model of CD performance and consider the effects that the proposed synaptic modification rule given by Eqs. (2) and (3) has on its behavior. We model the CD task as mediated by a local cortical column consisting of two interconnected subpopulations of excitatory and inhibitory neurons (Adini et al., 1997; Somers et al., 1998; Fig. 6) The activity of the excitatory (E) and the inhibitory (I) subpopulations is determined by the external feed-forward inputs (e and i , respectively), which are (non-linear) increasing functions of the stimuli contrast (C), and the recurrent interactions in the local network. When the contrast of the visual stimulus is increased, the resulting activity (E) also increases, enabling the discrimination between the contrasts. The CD threshold is controlled by the steepness of the relation between the activity (E) and the contrast. Assuming the threshold-linear gain functions for both subpopulations, the network activities follow the following dynamics (Wilson & Cowan, 1972):

$$\tau \dot{E} = -E + [e + J_{ee}E - J_{ei}I]_+ \quad (4)$$

$$\tau \dot{I} = -I + [i + J_{ie}E - J_{ii}I]_+$$

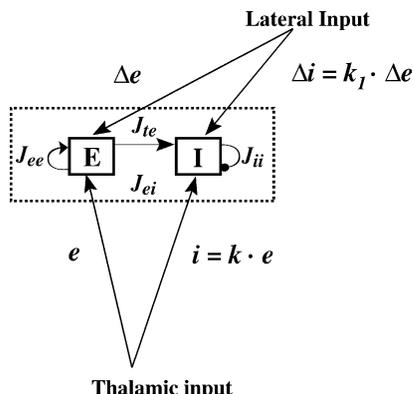


Fig. 6. A schematic representation of a cortical hyper-column (Adini et al., 1997, 2002), consisting of two interconnected sub-populations (E —excitatory, I —inhibitory), used here to model contrast discrimination. Both E and I populations receive external input from the thalamus (e, i) and from within the cortex ($\Delta e, \Delta i$).

where τ is the time constant of the dynamics that will be put to one in the following. If the sensory input from the eye is divided in a certain fixed proportion between the two populations ($i \equiv ke$; where k does not depend on the contrast), the steady state solution of Eq. (4) is given by

$$E = e \frac{1 + J_{ii} - kJ_{ei}}{\Lambda(J)} \quad I = e \frac{J_{ie} - k(J_{ee} - 1)}{\Lambda(J)} \quad (5)$$

with abbreviation $\Lambda(J) = J_{ei}J_{ie} - (J_{ee} - 1)(J_{ii} + 1)$. Eq. (4) was studied many times in the past, and we assume that the steady states solution given by Eq. (5) is a stable one with positive values of E and I . This requires that the following inequalities are satisfied (see Tsodyks et al. (1997) for details)

$$J_{ee} - 1 < J_{ii} + 1 \quad J_{ei}J_{ie} > (J_{ee} + J_{ii})^2/4 \quad (6)$$

that also automatically guarantees that $\Lambda(J) > 0$. In particular, this means that if recurrent excitation exceeds the destabilizing level ($J_{ee} > 1$), it has to be offset by strong enough inhibition. In this description, the contrast dependence of the network response is entirely determined by the contrast dependence of the feed-forward input e , with network interactions providing the overall scaling factors (Eq. (5)).

We now proceed to study the implications of the synaptic learning rule given by the Eq. (1) on the properties of the network. More specifically, we assume that connections $E \rightarrow I$ and $I \rightarrow E$ change according to this rule (for the other two types of connections, J_{ee} and J_{ii} and, this rule is not applicable since for them pre- and post-synaptic rates are always equal to each other). Since the dynamics of E and I is much faster than the dynamics of J_{ei} and J_{ie} , we can assume that for every presentation of the input, steady state of Eq. (5) is reached, and the corresponding values of E and I are used to update the strength of the connections. We therefore denote $J_{ei} = P_{ei}W_{ei}$; $J_{ie} = P_{ie}W_{ie}$, and substituting Eq. (5) into Eq. (2), to obtain the effective update equations

for the corresponding release probabilities:

$$\begin{aligned} \dot{P}_{ei} &= er_{ei}P_{ei}EI \frac{1 + J_{ii} - P_{ei}\{\varepsilon_{ei}W_{ie}P_{ie} + k[W_{ei} - \varepsilon_{ei}(J_{ee} - 1)]\}}{\Lambda} \\ \dot{P}_{ie} &= er_{ie}P_{ie}EI \frac{-k(J_{ee} - 1) + P_{ie}\{W_{ie} - \varepsilon_{ie}(1 + J_{ii} - kW_{ei}P_{ei})\}}{\Lambda} \end{aligned} \quad (7)$$

While these equations look rather tedious, they have the following general form:

$$\begin{aligned} \dot{x} &= er_x f(x, y) [-x(a_1 + b_1 y) + c_1] \\ \dot{y} &= er_y f(x, y) [y(a_2 + b_2 x) - c_2], \end{aligned} \quad (8)$$

where for brevity we replaced P_{ei} and P_{ie} with x and y . Function $f(x, y)$ takes positive values (it is equal to the product EI) and the constants in the brackets are all independent on e , namely:

$$\begin{aligned} a_1 &= k(W_{ei} - \varepsilon_{ei}(J_{ee} - 1)); a_2 = W_{ie} - \varepsilon_{ie}(1 + J_{ii}) \\ b_1 &= \varepsilon_{ei}W_{ie}; b_2 = k\varepsilon_{ie}W_{ei} \quad c_1 = J_{ii} + 1; c_2 = k(J_{ee} - 1) \end{aligned} \quad (9)$$

The first conclusion from this analysis is that equilibrium values for synaptic weights reached for repeated presentation of the sensory stimulus are independent of the contrast. However, the equilibrium values of x and y depend on the value of k , i.e. different division of external input between two sub-populations lead to different weights of the connections. Straightforward analysis of Eq. (8) shows that the equilibrium values (x_0, y_0) satisfy the following relations:

$$x_0 = \frac{\tilde{x}_0}{k}; y_0 = \tilde{y}_0 k \quad (10)$$

where \tilde{x}_0, \tilde{y}_0 do not depend on k . Looking back at Eq. (5) and recalling the meaning of variables x and y , we see that if the value of k changes, synaptic modifications work to compensate this change in terms of the slope of the input-dependence of E (both Λ and kJ_{ei} are invariant to transformation in Eq. (10)). For example, increasing k leads to smaller J_{ei} and larger J_{ie} , such that I grows faster with e , but the growth of E with e is the same as before the change. These results are compatible with our psychophysical findings. Indeed, practicing the CD task with isolated target is equivalent to stimulating the network with different contrasts but fixed value of k . This therefore leads to stable performance that is determined by this value of k . Surrounding the central target with flankers adds intra-cortical excitation to both of the populations responding to the central stimulus (Adini et al., 1997). If we assume that this intra-cortical input is more biased towards inhibitory subpopulation than the central input, this effectively increases the value of k . After the flankers are removed and the CD performance is measured again for the central stimulus alone, i.e. with the old value of k , the values of J_{ei} and J_{ie} are changed in accordance with Eq. (10), which in turn results in higher slope of the contrast dependence of E

(see Eq. (5)). According to our basic assumption, higher slope of this dependence is equivalent to better CD performance, as indeed observed psychophysically. To illustrate the working of this scenario, we simulate our psychophysical data using the well-known Naka–Rushton function (Naka & Rushton, 1966) to describe the thalamic input as a function of the stimulus contrast:

$$e = \frac{C^p}{C^q + A^q} \quad (11)$$

We chosen the parameter values $p=3.5$; $q=3$; $A=3.5$ and assumed that for a central input alone, $k=1.1$. The simulations for the ‘before’ practice curve were obtained using Eq. (5) with $J_{ee}=3.3$, $J_{ie}=4.1$, $J_{ii}=6$, and $J_{ei}=4.7$. If during the practice with flankers, the effective value of k is increased to 1.4, this leads, according to Eq. (10), to the new values of $J_{ei}=3.7$, $J_{ie}=5.2$ that we used in the ‘after’ simulations (but with the old value $k=1.1$, corresponding to central stimulus alone). All other parameters were the same as in the ‘before’ simulations. We have assumed that any two contrasts, C_1 and C_2 , can be discriminated if $E(C_2) - E(C_1) > 1$ (C in %contrast). The simulation results are presented in Figure 7.

Finally, we discuss the stability properties of the effective synaptic dynamics described by Eq. (8). In the above analysis, we assumed that these dynamics converge to a stable fixed point solution that correspond to the equilibrium point for the network. However, the stability of the fixed point is not guaranteed, as it depends on the parameters of the dynamics. Even if the fixed point is stable, approaching it after the stimulus change may involve damped oscillations. The stability of the fixed point solution can

be analyzed by linearizing Eq. (8) around this solution:

$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} = eE_0I_0 \begin{pmatrix} -r_x c_1 & -b_1 x_0^2 \\ b_2 y_0^2 & r_y c_2 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} \quad (12)$$

The stability of the fixed point solution of this system is determined by the eigenvalues of the matrix in Eq. (12), such that the dynamics is stable the real part of the eigenvalues are negative. One can see from Eqs. (9) and (12) that the stability requires that

$$r_{ei}(J_{ii} + 1) > r_{ie}k(J_{ee} - 1) \quad (13)$$

When this inequality is violated, the Hopf bifurcation occurs, where the fixed point solution gives birth to sustained oscillations. When the system is stable but close to Hopf bifurcation, synaptic dynamics can exhibit damped oscillations when approaching the equilibrium point after the change in the stimulus configuration.

5. Conclusion

Visual psychophysics was used to study learning in cortical networks. Of importance here is the context effects found in simple detection tasks, consistent with the rich intrinsic connectivity known to exist in the primary visual cortex. The implied network integrates local information to form activity patterns that correspond to global shape properties, such as extended contours and texture (Bonneh & Sagi, 1999a; Li, 2000). As such, they may provide a simplified, and relatively well defined, model network to study integrative functions of the neocortex where contextual information is critical to resolve ambiguities. These functions are essential for the formation of objects and concepts from the rich sensory data encountered during behavior. Experience has a critical role in these processes. In the visual system, surround effects are found to depend on the current behavioral goal and on past experience with the stimuli and task (Freeman, Sagi, & Driver, 2001; Ito, Westheimer, & Gilbert, 1998; Polat & Sagi, 1994b). Our goal is to expose the mechanisms underling this behavior.

Our results indicate that neocortical networks may adjust their intrinsic connectivity to prevailing stimulus configurations. In our model, we only considered the changes in the internal balance between excitation and inhibition in the local circuits, in response to additional lateral inputs coming from the surrounding stimuli. In future studies, it seems natural to extend this consideration to include the plasticity in long-range lateral interactions as well. The exact function of this context-dependent recalibration of connectivity is not very clear to us. One of the functions could be preserving stability of the visual system—simply changing the amplitude of the prevailing stimuli fails to cause the connectivity to change, preserving the plasticity to truly novel stimuli. Whether the particular combination of Hebbian and non-Hebbian plasticity rules

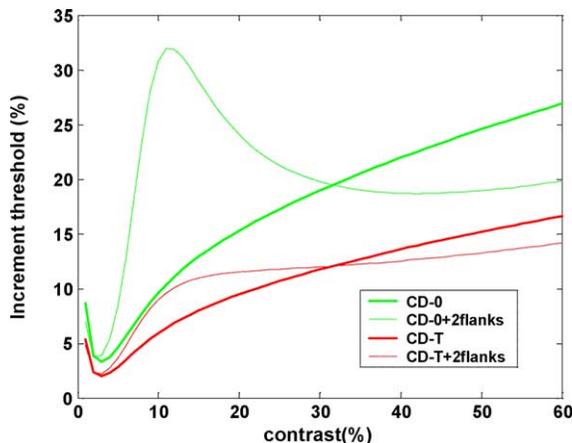


Fig. 7. Performance of the model on the contrast discrimination task before and after training with flankers. Also shown are discrimination thresholds in the presence of two flankers, simulating the psychophysical results shown in Fig. 5. See text for details Flankers effects were simulated by combining the thalamic and lateral e and i influences, thus effectively increasing k in a contrast-dependent manner. Compare with the experimental data presented in Fig. 5.

considered in this paper is in any sense optimal for representation of sensory world in the connectivity pattern of primary sensory areas, remains a challenge for future studies.

6. Experimental methods

There were three types of psychophysical experiments: (i) contrast discrimination (CD) experiment, (ii) chain experiment, and (iii) contrast discrimination with chain experiment. These experiments were described before (i: Dorais & Sagi, 1997; ii: Adini & Sagi, 2001; iii: Adini et al., 2002).

Contrast discrimination experiment. Contrast detection and discrimination thresholds were measured for a foveal Gabor Signal (GS: $\sigma = \lambda = 0.15$ or 0.2°). To measure the TvC (Threshold vs Contrast) function of the observers, we used 7–9 (depending on the experiment) different base contrasts (contrast pedestals) that spanned the contrast range 0–60%. In most experiments the different base contrasts were ordered from low to high within a session. Experiments showed no significant effect of contrast ordering.

Chain experiment. Contrast detection or discrimination thresholds were measured for a foveal Gabor Signal (GS) flanked on each side by a chain of 1–6 Gabor Signals. Thus the total length of a chain varied between 2 and 12 (not including the target). The target and the flankers were vertical Gabor Signals, forming a parallel configuration (shown in Fig. 2) with a spacing of 2λ (0.3°) or 3λ (0.45°). There were two types of chain stimuli: (i) with an empty space at target location (data shown in Fig. 4), and (ii) with an additional Gabor Signal at the target location introducing a base-contrast equal to flankers contrast (as in Fig. 2; data shown in Fig. 3).

Contrast discrimination experiments with chains. TvC curves were measured as in the *contrast discrimination experiment*, but with the target flanked by a variable number of Gabor Signals. Here, the chain contrast was kept fixed at 30% (data shown in Fig. 5). This method was used in the learning experiments (see Adini et al., 2002 for more details). Both the collinear and the parallel configurations were used in the experiments described here (3 observers, 2 with the collinear configuration and 1 with the parallel configuration).

Psychophysical procedure. A two Alternative Forced Choice (2AFC) paradigm was used. Each trial consisted of 2 stimuli presented sequentially, only one of which contained a target. Before each trial, a small white fixation circle was presented at the center of the screen. The observers, when ready, pressed a key to activate the trial sequence, which consisted of: (1) a no stimulus interval (500 ms), (2) a stimulus presentation (90 ms), (3) a no stimulus interval (1000 ms), and (4) a second presentation (90 ms). The observers' task was to determine which of the stimuli contained the target. An adaptive method was used to

determine the contrast threshold. Stimuli were displayed as gray level modulations on a computer monitor with an average display luminance of 50 cd/m^2 , in an otherwise dark environment. Stimuli viewed from a distance of 125 cm. More details can be found in Dorais and Sagi (1997) for the methods used to obtain the data shown in Fig. 1 and in Adini and Sagi (2001) for the data shown Figs. 3–5.

Stimuli. The basic stimulus element was a Gabor Signal (see inset in Fig. 1), described as:

$$\begin{aligned} GS(x,y) &= A \exp(-((x-x_0)^2 + (y-y_0)^2)/\sigma^2) \\ &\quad \times \cos(2\pi(x-x_0)/\lambda); \\ A &= I_0 C / 100 \quad (0 < C < 100); \end{aligned} \quad (14)$$

where I_0 is the mean screen luminance, C is the contrast parameter and (x_0, y_0) is the position of the GS on the screen. Each stimulus (see Fig. 2) was generated as a superposition of one or more GSs, added with the mean screen luminance (I_0).

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