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Plasticity of Spatial Interactions in Early Vision

1. INTRODUCTION

When a person is asked to perform a visual (or any other sensory) discrimination task it is often the case that he or she improves with practice, even on very simple tasks. This improvement occurs without any reinforcement and does not seem to involve conscious effort, but rather it seems to be controlled by some inherent subconscious process. During the last decade perceptual learning was shown to be involved in a variety of visual tasks: Stereoscopic vision,^{25,31} gratings detection,^{5,8} hyper-acuity,^{23,30} phase discrimination,⁶ motion detection,² texture discrimination (Karni and Sagi, this volume),^{1,13,14} search,³⁸ and pattern discrimination.²⁴ Some of these studies showed specificity of learning for location in the visual field^{2,8,14,24,25,30} (what was learned at one retinal location could not be used when stimulus was presented at another location), for orientation,^{1,2,8,14,20,30,31} spatial frequency,⁸ and direction of motion.² Though in most of these experiments learning was found to transfer across eyes (what was learned with one eye only could be used with the other eye), some studies showed only partial transfer² or absence of transfer,¹⁴ thus supporting a low-level anatomical site for the learning to take place. In some cases learning was found to persist for a few weeks,^{2,8} or even for years¹⁵ without

further practice. A new wave of studies provide more insight into the processes involved in perceptual learning. In particular, texture segmentation,^{1,14,15,16,17} lateral masking,²⁹ and hyperacuity^{7,30,40} are being studied providing interesting results. These experiments demonstrate again the specificity of learning for stimulus features. However, learning was found to be also specific for non-stimulus variables, such as the task used for training,^{1,16} implying higher level controls over learning. The existence of two types of learning, fast (binocular) and slow (monocular), was demonstrated,¹⁵ indicating learning at different levels of processing.¹⁶ The slow phase was found to require a consolidation period¹⁵ of about six hours, which, when during sleep time, was found to depend on the integrity of REM sleep stage.¹⁷

While all these studies show improvement of performance with time, and provide hints for the possible anatomical localization of the sensory modifications

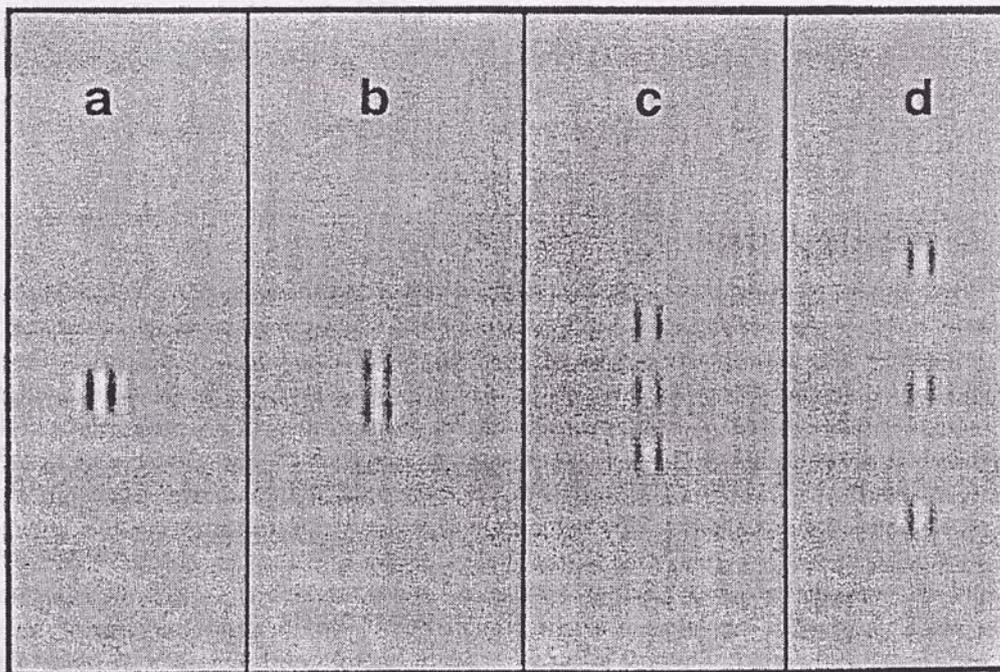


FIGURE 1 Stimuli configurations demonstrating some target to mask distances used in the present experiments. Distance (center to center as illustrated on the right) equals (a) 0λ , (b) 1.5λ , (c) 3λ , and (d) 6λ . Observers task is to detect the central patch, however, here target contrast (central patch) is somewhat enhanced for demonstration purpose.

involved, there is no clear idea as for the type of modifications and mechanisms involved. Recently, we have shown, using a lateral masking paradigm,^{27,28} that perceptual learning involves increased range of interactions in early vision.²⁹ In these studies observers were trained to detect a Gabor signal (see Figure 1) in the presence of two flanking high contrast but otherwise similar signals (masks). Target detection was found initially to improve by the presence of masks at a short distance only,²⁷ implying short-range interactions. Practice had the effect of a continuous increase of interaction range, in a way that long-range interactions could not be established before medium-range interactions were becoming effective. It was suggested that long-range interactions are produced by chains of local interactions. In this chapter we show that this type of learning is highly specific. Learning was found to be specific for eye, spatial frequency and retinal location (to within a neighborhood of half a degree). Thus, our results demonstrates that an early level of visual processing, which is dominated by local processes,³⁵ can be modified, even at adulthood, to detect long-range correlations.

2. METHODS

Observers were trained to detect a Gabor target flanked by two high contrast Gabor masks,^{27,28,29} with the distance varied during the course of the experiments (Figure 1). Stimuli were displayed as graylevel modulation on a Hitachi HM-3619A color monitor, using an Adage 3000 raster display system. The video format was 56 Hz noninterlaced, with 512×512 pixels occupying a $9.6^\circ \times 9.6^\circ$ area. The mean display luminance was 50 cd/m^2 in an otherwise dark environment. A two-alternative temporal forced-choice paradigm was used. Each trial consisted of two stimuli presented sequentially, only one of which had a target. Before each trial, a small fixation cross was presented at the center of the screen. When ready, the observers pushed a key to activate the trial sequence. This sequence consisted of a no-stimulus (i.e., uniform grey) interval (500 msec), a stimulus presentation (90 msec), a no-stimulus interval (1000 msec), and a second stimulus presentation (90 msec). The observer's task was to determine which of the stimuli contained the target. Auditory feedback, by means of a keyboard bell, was given on observers' error immediately following the response. A staircase method²⁸ was used to determine the contrast threshold. The observers' vision in both eyes was normal, with stimuli viewed from a distance of 180 cm.

3. RESULTS

3.1 INCREASING THE INTERACTION RANGE

Observers were trained with stimuli having different target to mask separations (samples can be seen in Figure 1). The range of distances used during each daily session was 0 to 12λ , and this was repeated few times per week, for a few weeks. The results show a slow increase in interaction range by up to a factor of two for different signal wavelengths: 0.075° , 0.15° (Figure 2), and 0.3° .²⁹ Assuming that receptive field size is two times its optimal wavelength²⁷ then the foveal filter integrates now inputs from far more than six times its receptive field size. A larger range of

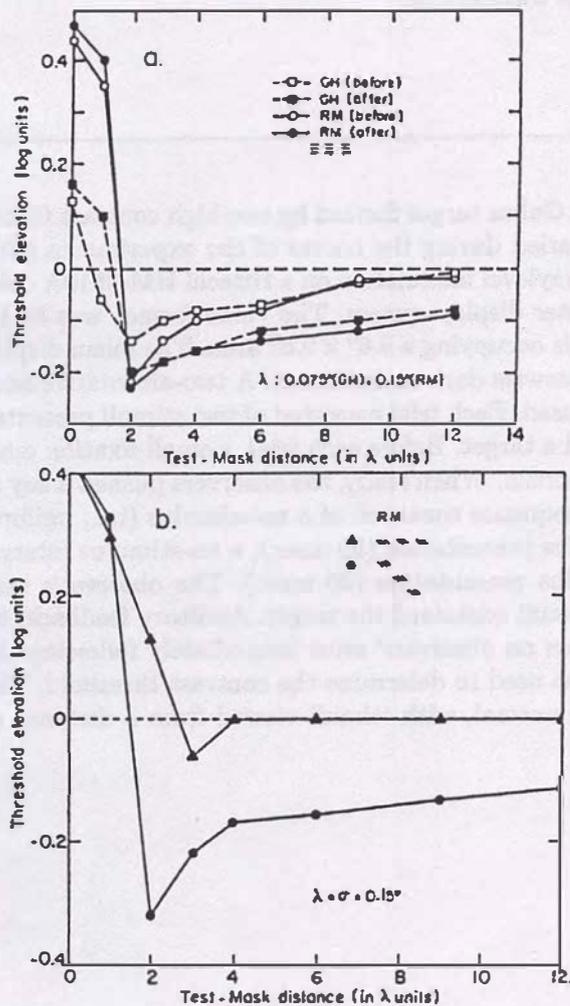


FIGURE 2 Dependence of target threshold on target-to-mask distance. Threshold elevation is computed relative to that of an isolated target. (a) Data is presented for horizontal target and masks arranged along the horizontal meridian, before (empty symbols) and after thirty sessions of practice (filled symbols), for two observers on two different λ 's. (b) Data is presented for diagonal target and masks arranged along the horizontal (\blacktriangle) or diagonal (\blacksquare) meridian. The same number of sessions, λ and σ as presented for observer RM in (a). Note that extensive practice on the noncollinear configuration resulted no change of enhancement range, indicating dependence of learning on already existing connections. (From Polat and Sagi²⁹; reprinted by permission of the authors.)

interactions, up to distances of 20λ , were observed when more extensive practice included these far distances.

3.2 EVIDENCE FOR A CONSOLIDATION PERIOD

Karni and Sagi^{15,16} showed that texture discrimination learning involves a latent period in which the effect of practice is being consolidated. Measurements showed that improvement in performance can be seen only when two practice sessions are separated by 6 to 10 hours.¹⁵ We have made similar measurements for lateral masking learning and present here results of repeated measurements of enhancement at a distance of 6λ . Enhancement is computed as the logarithm of the ratio between thresholds of the masked target and the unmasked (isolated) target. We found that enhancement gain is 0, 0.01, -0.01 , 0.14, and 0.09 for inter-session times of 1, 2, 6, 8, and 24 hours respectively (data samples taken from three observers).

3.3 THE CRITICALITY OF INTERMEDIATE CONNECTIONS

In all training sessions observers were presented with a variety of separations (0, 1, 2, 3, 4, 6, 9, 12λ). We have shown before²⁹ that, although the main effect of learning is an increased sensitivity for large distances, practicing on large distances ($4-12\lambda$) alone does not produce any learning effect. We have suggested that the increased range of interactions is obtained by chaining together local interactions. Practice has the effect of improving local connections, thus allowing for multiple transmission across several links (synapses).

Here, the necessity of intermediate connections in generating long-range interactions is being confirmed by using a sparse sampling of target to mask distances within each session. We divided the set of training into two subsets; The first included distances of 0, 2, 4, and 9λ and the second set included the 1, 3, 6, and 12λ . No learning effect was found when observers practiced on each of the two subsets separately (see Figure 3). On the contrary, here, practice had the effect of reducing enhancement at locations where previously exist. This effect can be attributed to weakening of local interactions. We suggest²⁹ that the efficacy of interactions between two units can be reduced by repetitive activation of one of them while the other unit is not active. Only when both units are active, their connections efficacy improves (Hebbian learning). These results provide further support to the idea that long-range interactions cannot be obtained, unless intermediate connections are established first.

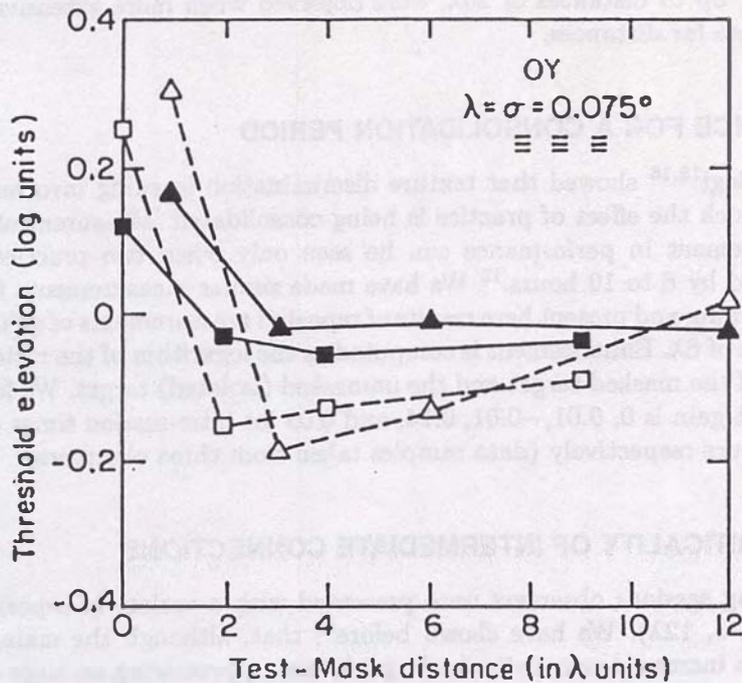


FIGURE 3 Data from experiments where an observer was trained on two sets of distances; the first included distances of 0, 2, 4, and 9λ (Δ before, and \blacktriangle after practice) and the second included distances of 1, 3, 6, and 12λ (\square before, and \blacksquare after practice). The observer practiced the two sets on the same days, but with one hour separating between them.

INTEROCULAR TRANSFER

We trained observers with one eye covered (monocular viewing), until an increase in the range of interactions was observed. When testing the untrained eye we found no increase in the interaction range (Figure 4(a-b)). This effect of no interocular transfer suggests a low-level anatomical loci for the learning effect to take place.¹⁴ To account for these results it is sufficient to assume that the synapses being modified receive input from monocular cells, thus it is possible that the post-synaptic side is binocular. However, dichoptic viewing experiments, where the target was presented to one eye while the two flanking masks to the other eye, support a monocular site (post-synaptic) for the spatial interactions to take place. These experiments show no interactions between target and masks.

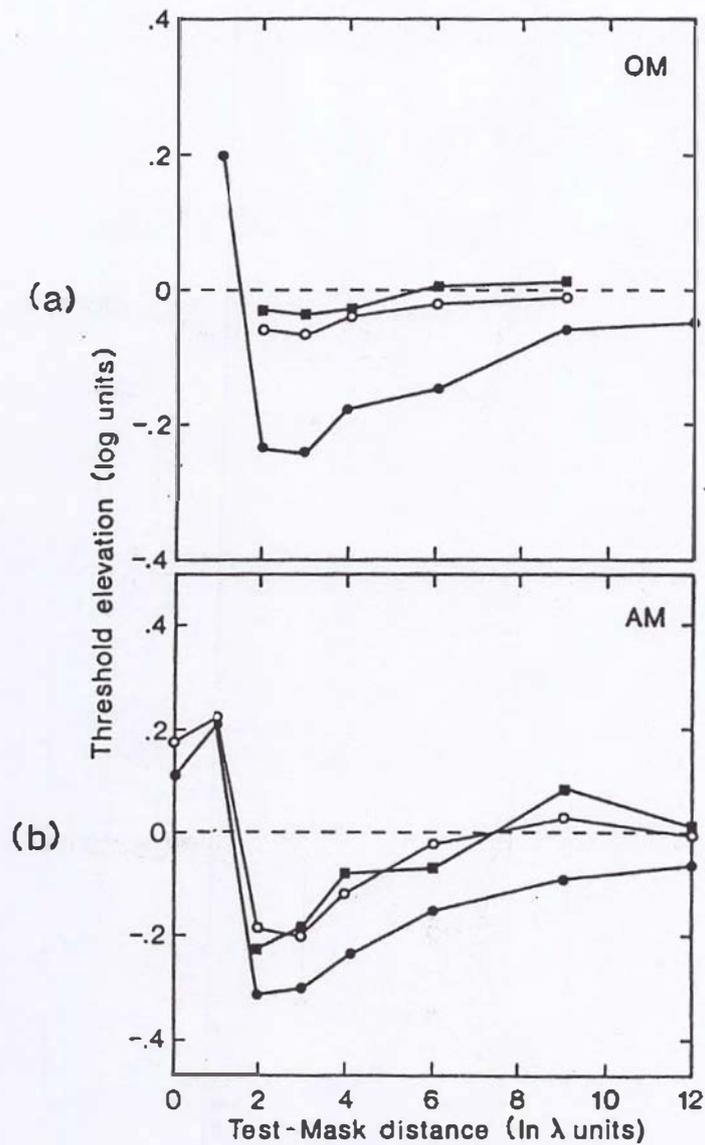


FIGURE 4 No interocular transfer of the learning effect. Range of interactions before (empty symbols) and after (filled symbols) practice. (a) Right eye before (\circ) and after (\bullet) practice; Left eye tested after practice of Right eye (\square). (b) Same as (a) but training with the Left eye (\circ , \bullet) and then a test of the Right eye (\square). (continued)

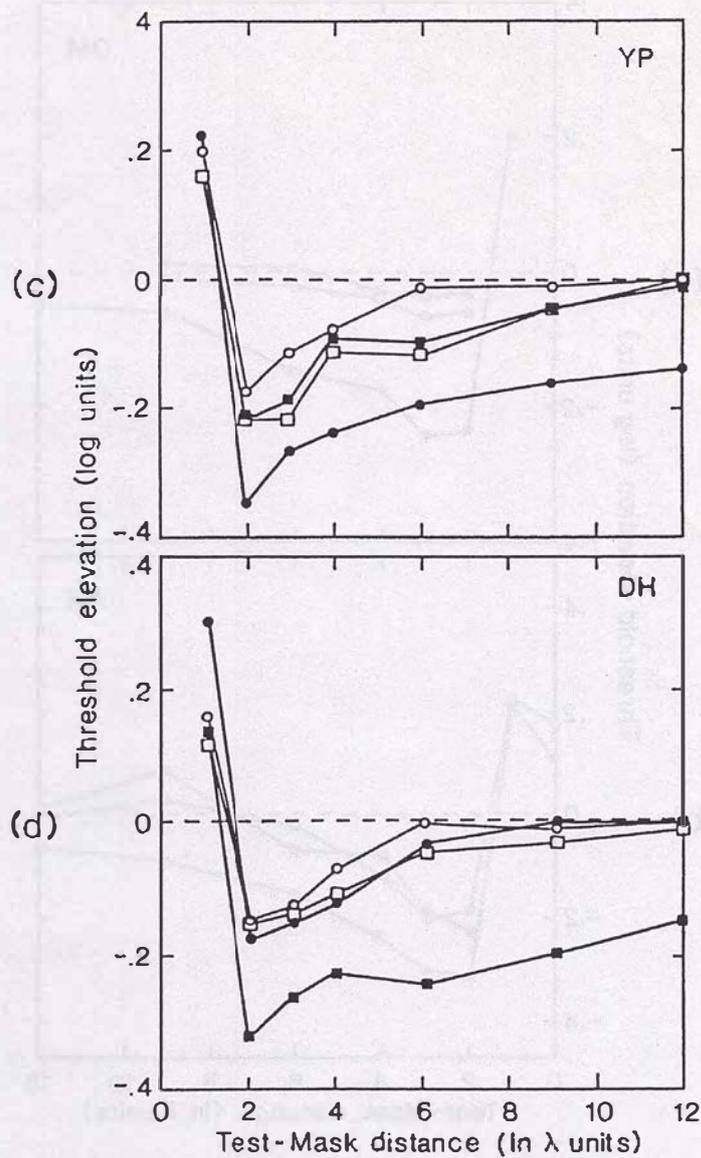


FIGURE 4 (continued) (c) The range of both eyes tested before (\circ, \square) and after (\bullet, \blacksquare) practicing of only one eye (R), indicating that the enhancement range of the untrained eye (L) is unaffected by practicing the other eye. (d) Same as (c) but practicing the Left eye.

3.4 SPATIAL FREQUENCY SPECIFICITY

Training with Gabor signals of one spatial frequency ($\lambda = 0.075^\circ$) and testing with a second spatial frequency ($\lambda = 0.3^\circ$) showed no transfer of interaction range (Figure 5(a)). A similar result was found when first training with lower spatial frequency ($\lambda = 0.3^\circ$) and then testing with the higher one ($\lambda = 0.075^\circ$) (Figure 5(b)).

3.5 RETINAL LOCATION

Few indications for retinotopic specificity were found: (1) When training with horizontal collinear configuration and testing with diagonal collinear configuration, retraining was needed to establish the effect of learning. This effect can also be attributed to orientation specificity. (2) Threshold measurements performed at a distance of 2λ (0.15°) distal to the largest practiced distance revealed no enhancement. However, an extension of the practice range up to this distance did show an effect of facilitation. Note that the magnitude of the spatial specificity is correlated with receptive field size, i.e., about 2λ .

4. DISCUSSION

Lateral masking experiments provide a very efficient and promising tool for exploring the architecture of early vision and plasticity. We believe that this paradigm is useful for exploring detailed connectivity of early visual processes and their dynamics. The basic results presented here are: (1) Thresholds are affected by target to mask distance (D): threshold increases for $D < 2\lambda$ and decreases for $2\lambda > D < 6\lambda$. (2) The range of enhancement can be increased up to at least 20λ with practice, when the observers are trained on all distances within one session. (3) The practice effect is specific for eye, orientation, spatial frequency and location.

The results obtained support an early visual system, composed of many spatial filters, each of which is selective for a limited range of orientations, spatial frequency and retinal locations.³⁵ Neighboring filters interact,²⁷ but mostly when they share the same orientations and spatial-frequency.²⁷ The longer range facilitatory interactions (see Figure 2) were observed so far only for collinear configurations, that is for cases where all interacting units are oriented along the line between them. Weaker interactions were observed for cases where local orientation is orthogonal to the connecting line.²⁸ Thus, these interactions can be used for line segmentations and for grouping, maybe serving the Gestalt rule of good continuation (Kovács and Julesz,¹⁹ this volume).¹⁸ The short-range effects ($0-2\lambda$) seen in Figure 2 may reflect a balance between different types of interactions. For this range one has to consider the direct effect of the masks on the target filter, an effect that depend on receptive field size and can produce both

suppression and facilitation, depending on mask contrast and target to mask distance. Recent experiments, covering a wider range of stimulus parameters, suggest

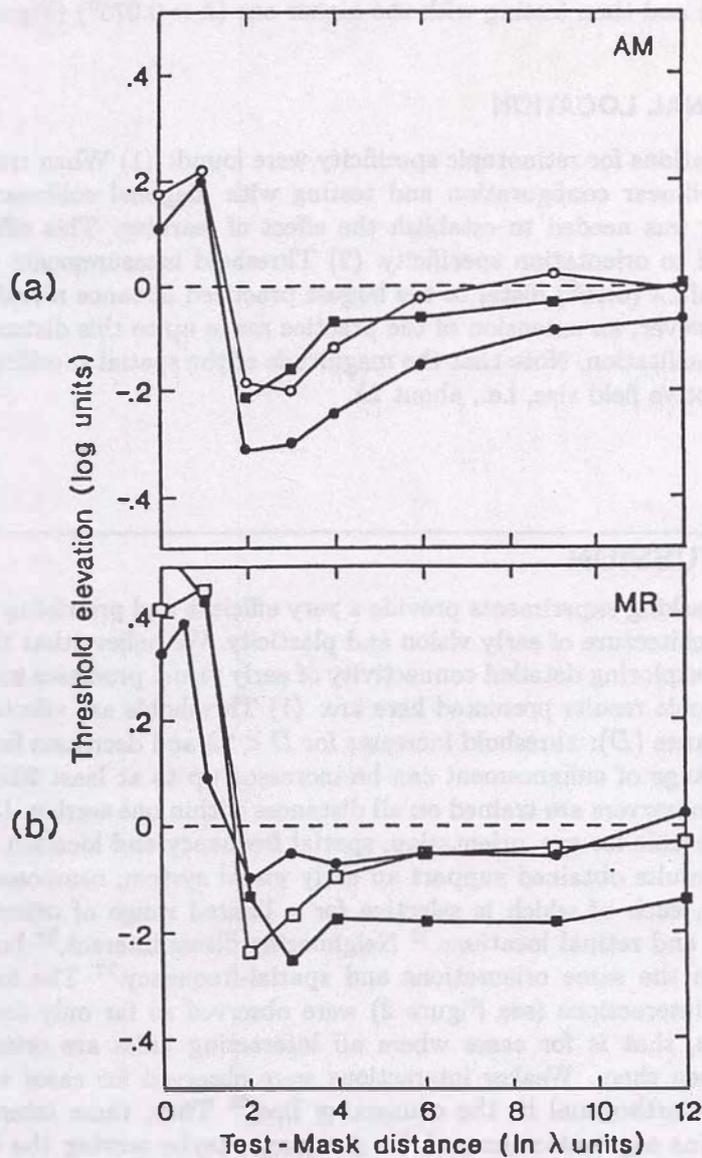


FIGURE 5 Specificity for spatial frequency. Training with one spatial frequency ($\circ, \bullet \lambda = \sigma = 0.075^0$) (a) or ($\square, \blacksquare \lambda = \sigma = 0.3^0$) (b), and testing with the other. Before ($\circ \square$) and \bullet after ($\bullet \blacksquare$) practice.

that short-range interactions are dominated by nonlinear inhibitory connections.⁴⁵

The main issue explored here is the stability of lateral interactions. The data indicate instability of interactions. Though the types of connectivity modifications taking place during long periods of practice are not understood yet, it seems that the main effect is an increase in interaction range. In some experimental conditions we observe a weakening of interactions (Figure 3; also see Polat and Sagi²⁹). Within the context of a network having short-range inhibitory connections and longer range excitatory connections, one has to consider modifiability of all interactions involved. Here we consider a model assuming plasticity of excitatory connections only,²⁹ though recent results,⁴⁵ showing disappearance of the suppression zone ($D < 2\lambda$) with practice, support also modifiability of inhibitory connections. We suggest that the increase of enhancement range reflects an increased range of interactions via a cascade of filters which are locally connected. Learning involves increasing efficacy of existing excitatory connections where connections are not distributed randomly but are arranged along the filter preferred orientation and orthogonal to it. Efficacy of connections increases only if both filters involved are being activated within a certain time window (of a few minutes). Efficacy decreases if only one filter is activated. These rules of learning are equivalent to Hebbian rules but with synchrony defined on a slower time scale.

Thus, in experimental conditions where all filters are being activated by external stimuli, all local connections improve their efficacy. However, when only a partial set of stimuli (masks) are presented, there is a reduction in efficacy of connections between activated filters and their nonactivated neighbors. This reduced efficacy reduces the chain's ability to transmit signals between filters across multiple connections, causing a loss of efficacy across all connections between mask activated sites and target activated sites. This scenario accounts for the phenomenon shown in Figure 3.

We believe that the laws of learning emerging from this study are applicable to human learning in general, and are not limited to perceptual learning or to procedural learning. The perceptual learning paradigm seems to provide a well-defined context to understanding the dynamics of learning, as we have a reasonably good understanding of brain processes operating on the sensory input. The high degree of specificity of visual learning for different image attributes indicates plasticity at sensory cortical areas as area V1. So far, only area V1 is known to contain cells which are highly local, orientation selective and monocular.⁴⁴ Also, recent electrophysiological studies show plasticity in a variety sensory cortical areas,^{21,22} such as visual,^{4,9,11,12,26,37} auditory,^{6,34,39,41} and somato-sensory.^{32,33} However, it is possible that, since multiple levels of processing are involved in a perceptual task, learning occurs at different processing levels. Of particular interest here is the distinction between "attentive" or selective processes and "nonattentive"³ processes. It is possible that in some cases attention is being used to filter out from the stimulus the relevant information for the task, and learning may reflect an improved selection or filtering.¹⁰ Indeed, recent studies show task dependent learning,^{1,16,36} however, monocular learning is difficult to reconcile with the 'attention' hypothesis

since attentive process cannot make a selection based on eye of origin information.⁴² According to recent findings,¹⁵ perceptual learning on a given task involves both types of learning, an initial phase of fast (within session) learning (binocular and probably task dependent), followed by a slower phase (monocular) requiring a few hours of consolidation. In some of the earlier learning experiments showing interocular transfer learning was found on the faster time scale,^{8,30} while experiments showing slower learning showed less interocular transfer.² The data presented here also indicate monocular and slow learning.

5. CONCLUSION

Psychophysical and electrophysiological studies provide evidence for plasticity of primary sensory areas. Perceptual learning seems to provide an excellent behavioral paradigm for exploring human learning, especially when coupled with current understanding of human vision. Perceptual learning seems to have two major components: fast (few hundreds of trials) and slow (days). The fast component seems to affect higher levels of processing (above the site of binocular integration) and probably involves top-down processes, improving the link between task dependent units and sensory units while selecting optimal sensory units for the task. Once these links become efficient, the task becomes "automatic" (nonattentive) and performance is then limited by sensory architecture only. The slow component seems to follow the fast one and involves low-level processes (monocular) within primary sensory areas. At this stage, links between sensory units are strengthened or weakened according to their activity correlations, thus establishing new associations and dissociations. First-order associations (via one link) are limited to direct connections, but higher order associations are possible by establishing chains of associations. Thus, while we are limited by system architecture in what we can perceive as direct associations, it is possible to perceive more complex percepts (or concepts) by indirect associations. Fast learning probably takes place on-line, when the stimulus is still effective or immediately after, but slow learning and the consolidation of associations seem to be performed off-line, for hours after stimulus presentation while the observer is not aware of the problem being solved. Though consolidation of associations may take place during day time, it seems that it also depends on processes that are active during REM (dream) sleep.

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