Spatial interactions in human vision: From near to far via experience-dependent cascades of connections

(short-range interactions/long-range interactions/lateral masking/learning/plasticity)

URI POLAT AND DOV SAGI*

Department of Neurobiology, Brain Research, The Weizmann Institute of Science, Rehovot 76100, Israel

ABSTRACT Perceptual learning has been shown to affect early visual processes. Here, we show that learning induces an increase in the spatial range of lateral interactions. Using a lateral masking/facilitation paradigm and bandpass-localized stimuli, we measured the interaction range before and after extensive training on a threshold detection task. For naive observers, target threshold was found to be facilitated by mask presence at distances up to six times the target period. However, practice had the effect of increasing the facilitation range by at least a factor of three. We suggest that the induced longer-range facilitation is a result of internal response transmission via a cascade of local connections. The data presented also show that this chain can be broken. These results suggest a plasticity in early vision governed by Hebbian-like rules.

When observers practice a visual discrimination or detection task they show improvement over time. Some of these improvements were found to be specific for stimulus orientation and target location (1–6), which suggests that early processing levels are involved in the learning process. Although this phenomenon was demonstrated on a variety of tasks, the rules underlying this learning still remain an enigma (7). Recent findings (6), showing absence of interocular transfer in texture discrimination tasks, lend further support for localizing perceptual learning to neural changes affecting low-level visual processing. As processes at these stages are mostly local (8, 9), learning may involve increasing the range of spatial interactions, either by strengthening of direct long-range connections or by increasing the efficacy of signal transmission via chains of local connections. Here we explore the plasticity of spatial interactions between local spatial processing units (filters) by using a lateral masking paradigm, in which observers show a large learning effect that is local, monocular, and orientation- and spatial-frequency-selective. We show here that interaction range increases continuously via chains of local interactions and suggest Hebbian-like rules for perceptual learning.

Local spatial interactions involved in visual processes can be explored by monitoring contrast detection thresholds for a localized periodic luminance-modulated target (Gabor signal) in the presence of spatially displaced high-contrast masks (also Gabor signals). Interactions were found for target and masks of similar orientation and spatial frequency and only within a limited spatial range (10). The interaction range was found to scale with target period (λ), and threshold increased for distances up to 2 λ and decreased for larger distances up to 6 λ. The longer-range facilitatory interactions were found mainly for target and masks arranged along the direction defined by the Gabor signal's local orientation (11). This optimal stimulus is presented in Fig. 1c and typical interaction effects (i.e., threshold elevation curves for stimuli with
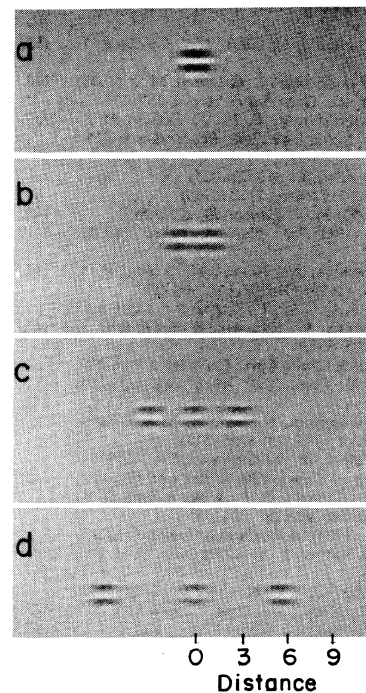
FIG. 1. Stimuli configurations demonstrating some target-to-mask distances used in the present experiments. Distance (center to center as illustrated on the right) = 0 λ (*a*), 1.5 λ (*b*), 3 λ (*c*), and 6 λ (*d*). Here target contrast (central patch) is somewhat enhanced for demonstration purpose; see ref. 8 for more details.

masks at different distances) for unpracticed observers are depicted in Fig. 2a (empty symbols).

METHODS

Observers were trained to detect a Gabor target flanked by two high-contrast Gabor masks (10), with the distance varied during the course of the experiments (Fig. 1). Stimuli were displayed as gray-level 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° × 9.6° area. The mean display luminance was 50 cd/m² 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 gray) interval (500 msec), a stimulus presentation (90 msec), a no stimulus interval (1000 msec), and a second stimulus presentation (90 msec). The observers' task was to

---

*To whom reprint requests should be addressed.

1206

Neurobiology: Polat and Sagi
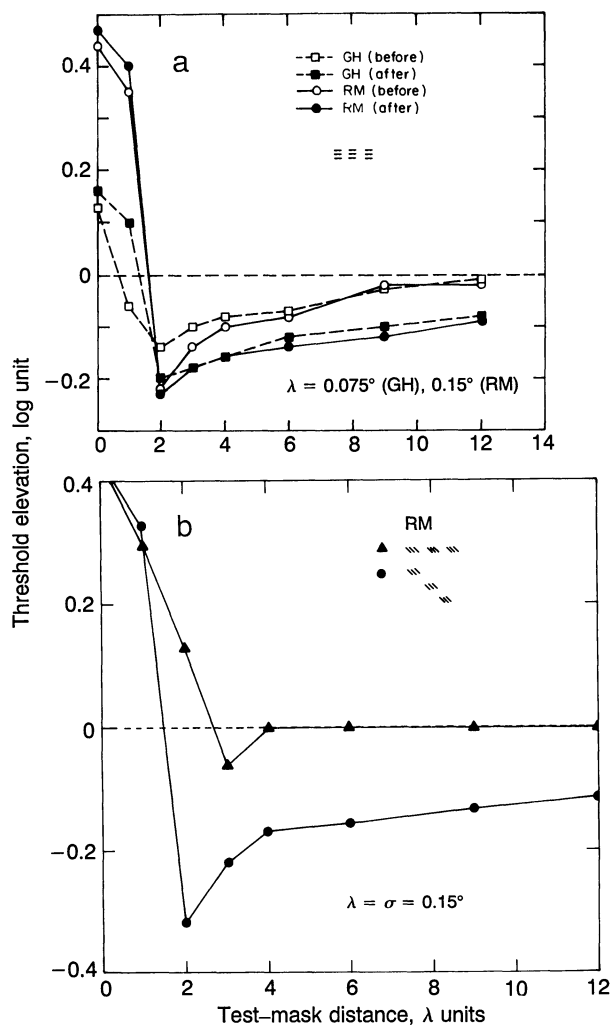
Proc. Natl. Acad. Sci. USA 91 (1994) 1207

FIG. 2. Dependence of target threshold on target-to-mask distance. Threshold elevation is computed relative to that of an isolated target. (*a*) Data are presented for horizontal target and masks arranged along the horizontal meridian, before (empty symbols) and after (filled symbols) practice for two observers on two different λs. (*b*) Data are presented for diagonal target and masks arranged along the horizontal (▲) or diagonal (●) meridian. The number of sessions, λ, and σ are the same as for observer RM in *a*.

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 method (10) was used to determined the contrast threshold. Ten observers with normal vision in both eyes participated, with stimuli viewed from a distance of 180 cm.

RESULTS

The learning procedure included training on contrast detection of a target stimulus flanked by masks at a range of distances (0–12 λ) during each daily session, and this was repeated several times per week. Results show an increase in interaction range up to a factor of two for different signal wavelengths (λ): 0.075°, 0.15° (Fig. 2*a*), and 0.3° (Fig. 3*c*). Data presented here reflect the initial state of interactions (open symbols) and the final state (filled symbols) after 40 sessions of practice. The temporal evolution of this learning effect follows a two-stage time course, previously described for texture discrimination learning (12), where the slow phase (described here) requires 8 hr to consolidate. Assuming that receptive field size is two times its optimal wavelength (13),

then at the termination of training, the foveal filter integrates inputs far more than six times its receptive field size. A larger range of interactions, up to distances of 20 λ, was observed when more extensive practice included these far distances. However, masks positioned at distances as small as 2 λ further away from the most distant training point failed to facilitate detection, meaning that learning is localized to within a single receptive field size.

We next examined whether such a learning effect could be found using stimuli configurations that previously were found to evoke only slight facilitation (11). These configurations include noncollinear arrangements of target and masks and, in particular, cases where target orientation was 45° away from the virtual line connecting the target and masks, thus suggesting that, in the untrained system, connectivity is constrained along the main axis defined by the receptive field orientation and somewhat orthogonal to it. Extensive training using diagonal target and masks positioned on the horizontal meridian failed to show any effect of learning, whereas the same diagonal signal positioned in a collinear configuration clearly showed a large increase in the range of enhancement (Fig. 2*b*). Thus, learning occurred in conditions where target and masks were aligned along their local orientation (or orthogonal to it) but not when local orientation was 45° from the global orientation. These results indicate that practice can only increase the efficacy of preexisting connections.

Detailed data to be described elsewhere show that this increase in range of spatial interactions for contrast detection is specific for eye, orientation, spatial frequency, and retinotopic location, suggesting that plasticity at very early levels of the cortical processing stream underlies the learning process (1–6). As this level is dominated by local interactions (8, 9, 14–16), the lateral enhancement in contrast detection may involve an increase in the range of connectivity between local retinotopic units, either by strengthening of direct long-range connections or by increasing the efficacy of signal transmission via chains of local connections. If our observed facilitation is mediated by a long direct connection connecting foveal and peripheral cells, we might expect that the increased range of interactions observed after practice reflects substantial improvement of direct far connections and, therefore, practicing on stimuli that would activate only units at a large separation should be as effective in driving practice-induced enhancement. Motivated by this hypothesis, we trained observers on sets of stimuli having relatively large separations between target and masks. No enhancement was found after 20 practice sessions (each being an hour long; Fig. 3*a*). An additional period of 10 practice sessions including medium-range separations also did not show any effect (Fig. 3*b*). However, completing the set with the addition of short-range separations presented at each session allowed for a dramatic effect of learning to take place at the large separation (Fig. 3*c*). Similar results were found for four more observers who were tested extensively on a single large separation; no range increase was found when practicing large separations only. Practice with only short and long (without the medium range) separations also failed to show increased enhancement range. Thus, the effect seems to require some integration over the whole range of separations. Note that each block of trials was dedicated to a single separation, and different separations were mixed during the course of a session, thus demonstrating integration over time for the learning effect, on a time scale of at least a few minutes. Further experiments utilizing multimask stimuli, in which each stimulus contained up to eight masks at different distances, showed faster learning. These results imply that intermediate connections are necessary for establishing long-range interactions, probably by creating a chain of interactions.
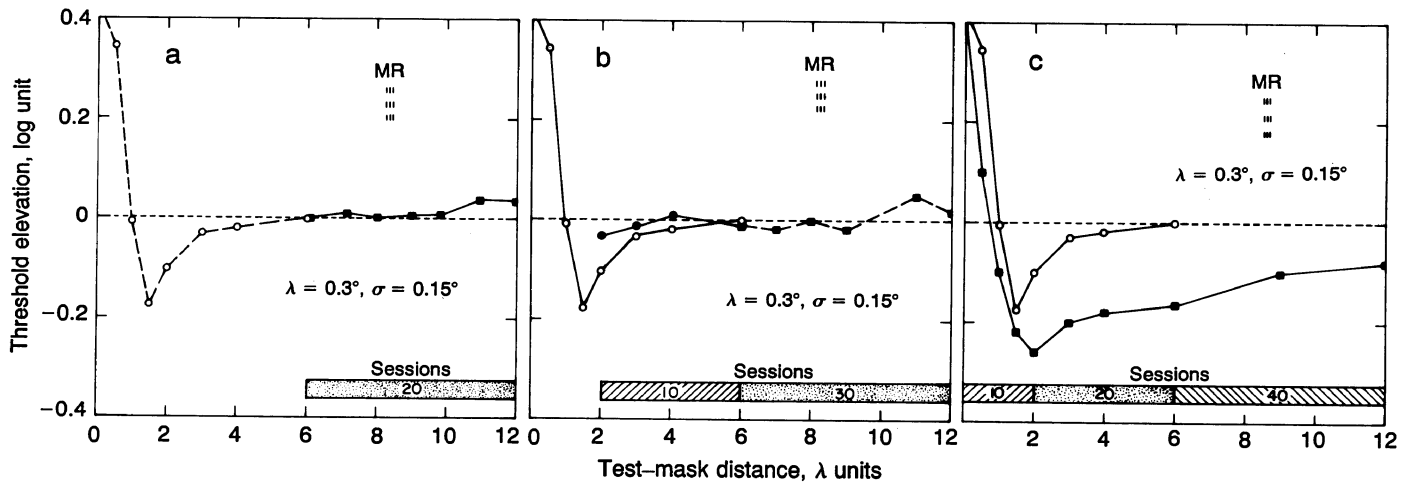
FIG. 3.   The same as in Fig. 2 but for vertical target and masks arranged along the vertical meridian. Here, only a limited set of distances was used in each session. The bottom bar illustrates the range and number of sessions used. Note that only in *c* can the effect of practice be seen.

While examining the data from sessions in which an incomplete set of separations between target and masks was presented (Fig. 3), we noticed that enhancement, where it had previously existed, tended to weaken (see Fig. 3*b*). This disruptive effect was confirmed by testing observers on a single separation within an already enhanced region. Here we found that practicing on a set of separations, restricted to the region of maximal enhancement, reduces enhancement at those distances and also at distances further away (Fig. 4*a*). In fact, practicing on a fixed intermediate separation (6 λ) destroys enhancement at all locations where it was previously existing (Fig. 4*b*). In contrast, practicing only on the zero- and one-wavelength separation (within the suppression range) does not have any effect on the enhancement region. Finally, extended practice on the complete range of separations in the same testing session does not destroy previously established enhancement. These results indicate that skipping intermediate separations breaks the chain of interactions.

DISCUSSION

We suggest that the increase of enhancement range reflects an increased range of interactions via a cascade of filters that are locally connected. If so, learning may involve increasing the efficacy of existing connections where connections are not distributed randomly but are arranged along the filter-preferred orientation and orthogonal to it. The efficacy of these connections increases only if an appropriate pair (along a chain) of interconnected local filters is being activated within a certain time window (probably within a few minutes). Efficacy decreases if only one filter is activated. These rules of learning are equivalent to Hebbian rules (17) but with synchrony defined on a slower time scale.

Our data can be accounted for by the following scenario: Each mask stimulus activates a filter (or a small set of filters or neurons). These filters are arranged topographically, so that masks corresponding to adjacent locations in the visual field activate adjacent filters. All interfilter connections are between adjacent filters. Activation of a filter by an external stimulus (e.g., a mask) is transmitted to adjacent filters, but with some attenuation. This attenuated signal can generate a filter response only in the nearby filters (at distances up to 4 λ, as indicated by the naive observers' data), but not in more remote filters when the system is unpracticed, unless the
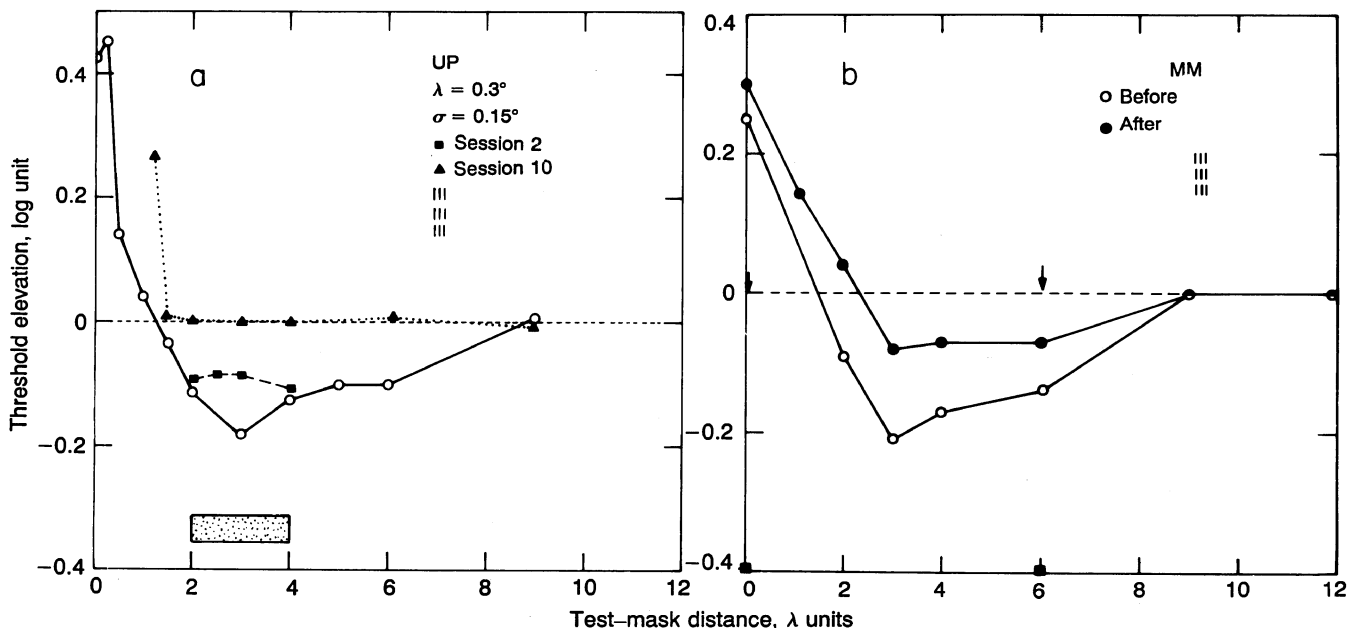

FIG. 4.   The same as Fig. 3, but the range used for practice is 2–4 λ in *a* and only two distances (0 and 6 λ) in *b*. The data show that the learning effect disappears at all separations after practicing on an intermediate range of distances.

receiving filter was already activated by another (external, in our case) stimulus within a critical time window.[†] In the case of successful activation of an interfilter connection, efficacy of connections increases (17) so that filters can be activated by their neighbors' neighbors with a high probability (P; $P <$ 1 between neighbors, but P^n across n connections). This higher internal response is sufficiently high to be transmitted successfully via the improved connections between farther-away mask-activated filters and the target filter. Failure to activate a neighboring filter (with probability of $1 - P$, in the absence of external input) reduces efficacy (18, 19). 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) is presented, there is a reduction in efficacy of connections between activated filters and their nonactivated neighbors (activation failures may also occur at the time between experimental sessions, but not that frequently due to the specific stimulus requirement). This reduced efficacy reduces the ability of the chain to transmit signals between filters across multiple connections, causing a loss of efficacy across all connections between mask-activated sites and target-activated sites. Regardless of the exact anatomical site of the associative network we propose, our data imply the existence of a processing stage in human vision in which most connections are local but modifiable so as to generate more complex patterns of activity that may contribute to evolving global percepts. Chains can be closed and activity may reverberate and significantly increase when the corresponding filters are stimulated, thus providing a possible mechanism for the recently observed enhancement in the detection of closed figures (20).

[†]Although the data presented here are for foveal targets, additional experiments show that the same pattern of enhancement exists for peripheral targets (at eccentricities of 3, 6, 9, and 12 λ as well as 3°). Maximal enhancement was always found when the mask was positioned at a distance of 2–3 λ from the target.

1. Ahissar, M. & Hochstein, S. (1993) *Proc. Natl. Acad. Sci. USA* **90**, 5718–5722.
2. Fiorentini, A. & Beradi, N. (1980) *Nature (London)* **287**, 43–44.
3. McKee, S. P. & Westheimer, G. (1978) *Percept. Psychophys.* **24**, 258–262.
4. Ramachandran, V. S. & Braddick, O. (1973) *Perception* **2**, 371–376.
5. Poggio, T., Fahle, M. & Edelman, S. (1992) *Science* **256**, 1018–1021.
6. Karni, A. & Sagi, D. (1991) *Proc. Natl. Acad. Sci. USA* **88**, 4966–4970.
7. Dudai, Y. (1989) *The Neurobiology of Memory* (Oxford Univ. Press, Oxford).
8. Rubenstein, B. S. & Sagi, D. (1990) *J. Opt. Soc. Am. A Opt. Image Sci.* **7**, 1632–1643.
9. LeVay, S. (1988) *Prog. Brain Res.* **75**, 147–161.
10. Polat, U. & Sagi, D. (1993) *Vision Res.* **33**, 993–999.
11. Polat, U. & Sagi, D. (1994) *Vision Res.* **34**, 73–78.
12. Karni, A. & Sagi, D. (1993) *Nature (London)* **365**, 250–252.
13. Olzak, L. & Thomas, J. P. (1986) *Handbook of Perception and Human Performance I*, eds. Boffand, K. R., Kaufman, L. & Thomas, J. P. (Wiley, New York), Chapter 7.
14. Gilbert, C. D. & Weisel, T. N. (1979) *Nature (London)* **280**, 120–125.
15. Ts'o, D. & Gilbert, C. D. (1986) *J. Neurosci.* **6**, 1160–1170.
16. Mallach, R., Amir, Y., Bartfeld, E. & Grinvald, E. (1992) *Soc. Neurosci. Abst.* **134**, 14.
17. Hebb, D. O. (1949) *Organization of Behavior* (Wiley, New York).
18. Stent, G. S. (1973) *Proc. Natl. Acad. Sci. USA* **70**, 997–1001.
19. Ahissar, E., Vaadia, E., Ahissar, M., Bergman, H., Arieli, A. & Abeles, M. (1992) *Science* **257**, 1412–1415.
20. Kovács, I. & Julesz, B. (1993) *Proc. Natl. Acad. Sci. USA* **90**, 7495–7497.