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)

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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.](image)

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

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Fig. 2. Dependence of target threshold on target-to-mask dis-
tance. 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 ob-
servers’ error immediately following the response. A stair-
case method (10) was used to determined the contrast thresh-
old. Ten observers with normal vision in both eyes partici-
pated, with stimuli viewed from a distance of 180 cm.

RESULTS

The learning procedure included training on contrast detec-
tion 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. 2a), and 0.3° (Fig. 3c).
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. 2b). 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 retin-
отopic location, suggesting that plasticity at very early levels
of the cortical processing stream underlies the learning pro-
cess (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
reinotopic units, either by strengthening of direct long-range
connections or by increasing the efficacy of signal transmis-
sion via chains of local connections. If our observed facil-
itation is mediated by a long direct connection connecting
foveal and peripheral cells, we might expect that the in-
creased range of interactions observed after practice reflects
substantial improvement of direct far connections and, there-
fore, 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.
3a). An additional period of 10 practice sessions including
medium-range separations also did not show any effect (Fig.
3b). 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 separa-
tion (Fig. 3c). 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 interac-
tions.
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. 3b). 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. 4a). In fact, practicing on a fixed intermediate separation (6 λ) destroys enhancement at all locations where it was previously existing (Fig. 4b). 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.\(^1\) 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 (\(P_i; P < 1\) between neighbors, but \(P^m\) 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 \(1 - P_i\), 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).

\(^1\)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 \(\lambda\) as well as 3\(^\circ\)). Maximal enhancement was always found when the mask was positioned at a distance of 2–3 \(\lambda\) from the target.

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