



Long-lasting, long-range detection facilitation

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Abstract

We examined the time course of threshold reduction in the Gabor lateral masking paradigm. Contrast detection thresholds were measured (2AFC) for a briefly presented (36 ms) foveal Gabor signal (GS), preceded by a presentation (90 ms) of two high-contrast GS flanked masks, with stimulus onset asynchrony (SOA) varying from 0 to 16290 ms. Using target-to-mask separations of 3λ and 12λ ($\lambda = 0.15^\circ$, GS wavelength), the 3λ separated GS masks enhanced target threshold by 0.25 log units at SOA = 0 and by 0.17 log units at 2700 ms. At 12λ separation, threshold was enhanced by 0.11 log units at SOA = 0 and by 0.14 log units at 2700 ms. Long-range (12λ) and short-range (3λ) enhancements persisted for over 16 s. Delayed and simultaneous enhancement depended on the stimulus configuration (maximal for collinear target and masks), local parameters (orientation, spatial frequency and phase), and the presented eye (dichoptic versus monoptic). The results suggest that spatial filters in early vision retain an input trace far beyond the perceptual integration range. This trace may subserve the consolidation of filter activity into long-term memory. © 1998 Elsevier Science Ltd. All rights reserved.

Keywords: Gabor signal; Stimulus onset asynchrony; Long-range detection

1. Introduction

Responses of the human visual system to spatial-temporal patterns are frequently described as the parallel operation of multiple localized filters [1,2]. These filters operate independently in separate regions, and each is selectively tuned to spatial frequency [3,4] and orientation [5,6]. Recent studies indicate the existence of spatial interactions between adjacent filters [7–10], implying both inhibition and facilitation, depending on spatial separation [11]. Polat and Sagi [12] tested contrast detection thresholds using a Gabor signal (GS) target with laterally located GS masks (lateral masking). Threshold was found to increase (suppression) with high-contrast lateral masks located less than a distance of two wavelengths (2λ) from the target. In contrast, larger distances up to 9λ produced lower thresholds (facilitation), the facilitation being maximal at a mask distance of 3λ . This enhancement was found to be

spatial frequency- (± 1 octave) and orientation- ($\pm 15^\circ$) specific [12]. Furthermore, specificity to spatial configuration was observed, with enhancement being maximal for co-oriented and co-axial target and masks, that is for collinear configuration [13]. Corresponding physiological evidence indicates that the neural basis for these spatial interactions exists in the primary visual cortex [14,15].

This study addresses the temporal properties of spatial interactions. Considering the dynamic nature of spatial (lateral) interactions leading to short-term memory [16] and perceptual learning [17], one may expect to find some delayed interactions between filters. Here, we use the forward masking paradigm with a time delay between the mask and target stimuli. We focus on the effect of delayed interaction in a time region beyond temporal summation (≈ 300 ms) [18–21], and within the range of visual short-term memory (seconds-to-minutes) [16,22–24]. Particularly, we ask whether there is a delayed facilitation which may point to temporal characteristics of filter activity leading to short-term memory. The answer to this question would clarify an association between early visual perception and visual memory.

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2. Methods

2.1. Apparatus

Stimuli were presented as gray level modulation on a Philips 17A dual autoscans color monitor with 3×8 bits, using an Adage 3000 raster display system. The video format was 56 Hz non-interlaced, with 512×512 pixels occupying a $9.6^\circ \times 9.6^\circ$ area. The mean display luminance was 43 cd/m^2 . Stimulus generation was controlled by a Sun-3/140 workstation and the stimulus display by the Adage local processor. Gamma correction was applied using 10-bit lookup tables and DACs. The stimuli were viewed binocularly from a distance of 125 cm in a dark environment. In dichoptic/monoptic experiments, stimuli were presented on a SONY multi-scan TC color monitor, using a Silicon Graphics Crimson Reality Engine system. The video format was 120 Hz interlaced, with 1280×450 pixels for each eye occupying a $9.56^\circ \times 6.72^\circ$ area. Stimuli were viewed with CrystalEyes E-1 stereo glasses with optic shutters that alternate in 120 Hz synchronized with the monitor. A 12-bit RGB mode was used, in which 12-bit pixels were converted by dithering into 10-bit values and then by a 10-bit Gamma correction into 8-bit RGB DACs. The mean display luminance was 40 cd/m^2 . Stimulus generation and display was controlled by a SGI/Reality Engine workstation. The viewing distance was 100 cm.

2.2. Stimuli

The stimuli consisted of three Gabor signals (GS) arranged vertically or horizontally. The luminance distribution of a GS is determined by

$$G_\theta(x, y, t | x_0, y_0, t_0) = \cos\left(\frac{2\pi}{\lambda}((x - x_0)\cos\theta + (y - y_0)\sin\theta)\right) \times \exp\left(-\left(\frac{(x - x_0)^2 + (y - y_0)^2}{\sigma^2}\right)\right) \times T(t | t_0, \text{du}).$$

with x and y being the horizontal and vertical coordinates, respectively, and $T(t)$ a temporal square pulse. The spatial location of GS is determined by x_0 and y_0 , its orientation by θ (in radians), and its wavelength by λ . The S.D. of the Gaussian envelope is given by σ . For the basic stimuli used in the experiments, $\lambda = 0.15^\circ$ and $\sigma = \lambda$ were kept constant. The target signal was presented at the fixation point location (x_0, y_0) , with vertical ($\theta = 0^\circ$) orientation. The luminance distribution of three GSs is described by

$$I(x, y, t | x_0, y_0, t_0) = I_0 + A_t G(x, y, t | x_0, y_0, t_{\text{soa}}) + A_m G(x, y, t | x_0, y_0 - \delta y, t_0) + A_m G(x, y, t | x_0, y_0 + \delta y, t_0).$$

with A_m and A_t being the mask and target amplitudes, respectively, t time delay ($t_0 = 0$: initial time at mask presentation, t_{soa} : from mask to target), and I_0 the average screen luminance. The three GSs were presented on the vertical median by varying δy . Mask amplitude (A_m) was 26% of the average luminance ($0.26I_0$). Contrast phase of mask and target was either equal ($A_m = A_t$) or opposite ($A_m = -A_t$). In the dichoptic/monoptic experiment, a relatively high contrast mask ($0.40I_0$) was used. The distance between the mask and target GS (δy) was fixed in each block of trials, being either 3λ ('short distance') or 12λ ('long distance').

2.3. Experimental procedure

A stimulus sequence consisted of the mask GSs, followed by a target GS after a temporal delay (stimulus onset asynchrony: SOA, defined as the time between mask and target onsets). Contrast thresholds for the targets were measured using a temporal two alternative forced choice (2AFC) procedure. Each trial consisted of two stimulus sequences, only one of which had a target. Before each trial, a fixation cross ($0.32^\circ \times 0.32^\circ$, 90 cd/m^2) was presented at the center of the screen. When ready, observers pressed a key activating the trial sequence (Fig. 1): a uniform luminance interval (450–900 ms, randomized, 1 ms bin), a first mask interval (90 ms), a uniform luminance interval (inter-stimulus interval or ISI = SOA – 90 ms), a first target interval (36 ms), a uniform luminance interval (1720–2160 ms, randomized), a second mask interval (90 ms), a uniform luminance interval (SOA – 90 ms), and a second target interval (36 ms). Both mask intervals contained mask GSs, but only one target interval contained a target GS. Two experimental conditions were employed: the forward masking (priming) condition, in which the mask GSs were presented prior to the target, and the control condition, in which masks were not presented ($A_m = 0$). To minimize temporal uncertainty, all mask and target intervals contained two peripheral crosses in both masking and control conditions ($0.46^\circ \times 0.46^\circ$, 90 cd/m^2 , located randomly in the area between 1.7° and 0.85° from the target, aligned at a direction of $\theta = -45^\circ$ but of $\theta = 45^\circ$ in mask displays; see Fig. 1). When SOA = 0, mask and target intervals overlapped for the initial 36 ms, with the mask continuing for another 54 ms. The observer's task was to determine which of the stimuli contained the target (detection task). Auditory feedback, by means of a keyboard bell, was given for an observer's error immediately after the response.

Target contrast threshold was determined using a staircase method, in which target amplitude (A_t) was increased by 0.1 log units in trials following an erroneous response and decreased by 0.1 log units following three consecutive correct responses. A staircase se-

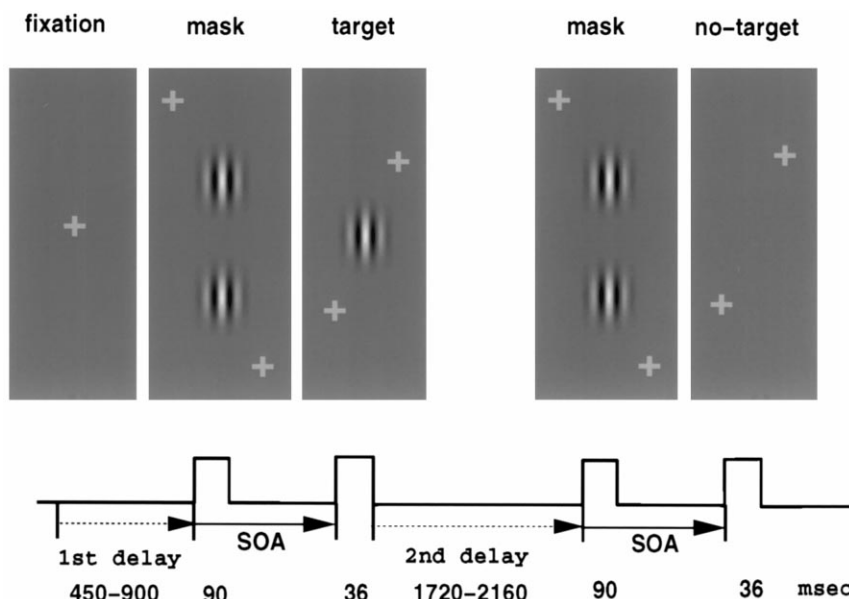


Fig. 1. GS stimuli and their time course in a single 2AFC trial. First, a fixation point appeared, then two flanked mask (prime) GSs (no GSs in the control condition) appeared on the screen. After a temporal delay (SOA), a target GS appeared (or did not) in the fovea. Mask and target displays contained two peripheral crosses to minimize temporal uncertainty (size and distances are not in scale in this figure). Following a 2nd delay, the mask target/no-target sequence was repeated. Target GS appeared either at the first or the second part of the trial. The observers were asked to indicate which sequence (first or second) contained the target. The intervals between the fixation and the first mask (1st delay), and between the first target and the second mask (2nd delay) were randomized.

quence was terminated after eight amplitude reversals (a block of trials) with the log-amplitude values at the last six amplitude reversals averaged to yield a threshold estimate. Threshold elevation was computed relative to the detection threshold of the target GS in the absence of the mask GS at the same SOA (control, mask amplitude $A_m = 0$). The initial target amplitude (A_t) was set at about 1.5 times the control contrast.

A session, consisted of groups of blocks, lasted approximately 1 h. Each block contained about 60 trials. Three major experiments were employed, where different parameters were manipulated separately; (1) a mask distance experiment, where the distance between mask and target was either 3λ , 12λ , or no mask (control). These composed a group of triple blocks, in which only one SOA (0 ms = simultaneous, 90, 144, 234, 324, 450, 684, 900, 1800 and 2700 ms) was tested. The order among 3λ , 12λ , and control was randomized within each triple block. SOAs were increased gradually from shorter to longer. Longer SOAs, from 4500 to 16290 ms, in addition to shorter SOAs (0–1800 ms), were tested for observer YT. Shorter distances (1λ and 0λ), in addition to the longer distances (3λ and 12λ), were tested for observer MD. In both experiments, the same triple block procedure was used. (2) A feature-selectivity experiment, where orientation, spatial frequency, or contrast phase of masks were, respectively, altered while target parameters were kept as before. In the orientation condition, horizontal ($\theta = 90^\circ$) masks were

used, and the target orientation was vertical ($\theta = 0^\circ$). In the spatial frequency condition, higher mask spatial frequency (13.3 cpd, $\lambda = 0.075^\circ$) compared with the target (6.7 cpd, $\lambda = 0.15^\circ$) was used. In the contrast phase condition, a mask phase opposite to the target ($A_m = -A_t$) was used. These conditions, in addition to control conditions, composed a group of four blocks, in which one SOA was tested. The order of the four conditions was randomized within a four block sequence. SOAs were increased from 0 to 1800 ms. Mask distance was fixed at 3λ . (3) A monoptic/dichoptic experiment, where masks were presented either to the same eye as the target (monoptic masking conditions, mask–target relationship: left–left or right–right) or to different eyes (dichoptic masking conditions, left–right or right–left). Crosses in mask intervals were presented to one eye together with the mask (masking condition) or without mask (control condition). Monoptic/dichoptic masking and monoptic/dichoptic control conditions for left/right eyes composed a group of eight blocks, in which one SOA (among 167, 336 and 867 ms) was tested. The order of masking and control conditions was randomized within an eight-block sequence. SOAs were increased from shorter to longer. Mask distance was fixed at 3λ . Each datum point was repeated at least three times. Five observers (AK, OS, MD, SC, and one of the authors, YT) participated in the experiments. The first four observers were college students (age, 22–26 years), being naive as to the purpose of the experiments.

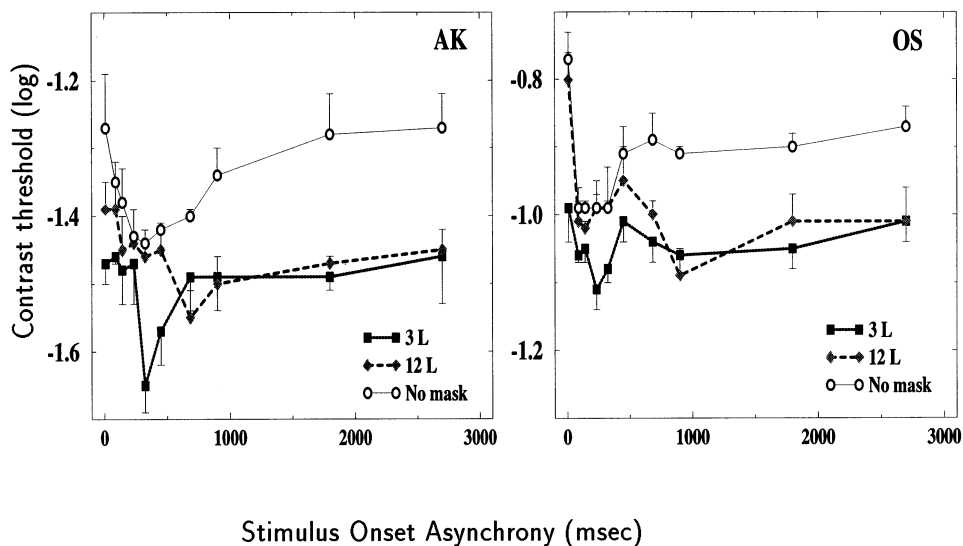


Fig. 2. Contrast detection threshold as a function of SOA for two observers (AK, OS). Configurations of mask and target GSs were collinear (co-oriented and co-axial). Performance shows a time dependence, with temporal variations depending on the mask distance. Error bars show 1 S.E.M. Each threshold estimate is based on three measurements.

3. Results

3.1. Mask distance experiment

Each session consisted of groups of triple blocks, each group consisting of three blocks testing one SOA, and three conditions: 3λ , 12λ , and control (see Section 2). Contrast detection thresholds for target GSs are plotted as a function of SOA in Fig. 2. Detection thresholds are shown for the control condition and for the masking (priming) condition with the near (3λ) and the far (12λ) GS masks (Fig. 2). The control thresholds first decreased until about 300 ms of SOA, and then increased toward the initial level after 600–900 ms of SOA. This ‘dip’ occurred presumably because of a temporal cuing effect of attention [25,26] (see Section 4). The forward masking curves show improved sensitivity at SOA = 0 ms relative to control, depending on distance. The enhancement for both mask distances is further improved with increasing SOA. The initial improvement in sensitivity developed slower in SOA in the forward masking condition, compared with the control condition, with optimal SOA depending on distance. Lowest thresholds for the 12λ configuration were obtained around an SOA of 800 ms, while for the 3λ configuration they were about 300 ms.

To illustrate the net masking effect, the data were replotted in Fig. 3 in terms of threshold elevation (the difference between mask thresholds and control). Threshold reduction (facilitation) was observed when SOA = 0, the magnitude being about 0.2–0.25 log units, in agreement with Polat and Sagi [12]. Facilitation decreased during the first 500 ms of SOA, however, longer delays yielded a significant and consistent facili-

tation, lasting as long as 2700 ms. This facilitation sometimes reached the initial values obtained at SOA = 0 ms. For the 12λ configuration, larger delays yielded even greater threshold reduction than simultaneous presentation. To test the temporal range of the masking effect, longer SOAs were tested; threshold reduction was observed up to SOA of 16290 ms (≈ 16 s), the largest SOA tested, for both the ‘near’ and the ‘far’ distances (Fig. 4). Note that facilitation is observed at an SOA more than 100 times longer than typical perceptual integration times [18,21].

The masking effect was also tested with shorter distances (0λ and 1λ ; for 0λ two mask GSs were overlapped, yielding a total mask amplitude of $0.52I_0$). A suppression was observed both with 0λ and 1λ distances at SOA = 0 ms, which is consistent with Polat and Sagi [12]. The suppression disappeared (0λ) or turned into facilitation (1λ) as SOA increased, indicating that high contrast masks (primes) at the target position (0λ) did not produce a significant long-term trace (Fig. 5). This is the first demonstration of a forward masking (or priming) effect by preceding flanking Gabor masks. Note that this effect occurred both at larger spatial distances (= long-range, 12λ) and at longer temporal delays (= long-lasting, ≈ 16 s) than previously reported [12,21].

3.2. Feature selectivity experiment

In this experiment, orientation, spatial frequency, and contrast phase of masks were altered to test feature specificity. Each session consisted of groups of four blocks, each group of blocks testing one SOA and four conditions: orientation, spatial frequency, phase and control (see Section 2).

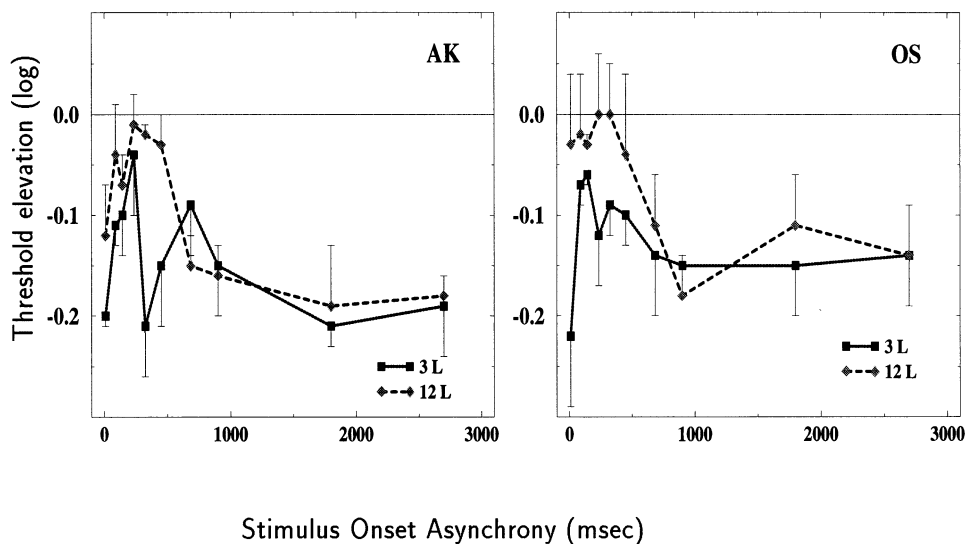


Fig. 3. Threshold elevation as a function of SOA for two observers (AK, OS). Data from Fig. 2 are replotted relative to control thresholds. Note that enhancement is much reduced with small delays (SOA < 500 ms), but increases with larger delays. Error bars show 1 S.E.M. of differences between masking and controls conditions.

3.2.1. Orientation specificity

In the orientation condition, where the orientation of the masks was horizontal ($\theta = 90^\circ$) while the target orientation was vertical ($\theta = 0^\circ$), threshold reduction was not observed (thresholds were at about the same level as the control) for any SOA, except at an SOA of 0 and 90 ms for observer OS (Fig. 6). This indicates that the masking effect is orientation specific.

3.2.2. Spatial frequency specificity

In the spatial frequency condition, where the spatial frequency of the masks was high (13.3 cpd , $\lambda = 0.075^\circ$)

compared with the target (6.7 cpd , $\lambda = 0.15^\circ$), threshold reduction was not observed for any SOA except for an SOA of 0 ms (Fig. 6). This shows that the masking effect is spatial frequency specific.

3.2.3. Phase specificity

In the contrast phase condition, the contrast phase of the masks was opposite to that of the target. At an SOA of 0 ms, threshold was found to be almost the same as with the same phase mask (facilitation). This is consistent with Zenger and Sagi [27], suggesting a ‘pooling effect’ from the ‘indirect’ masking source [28]. After a delay (SOA $\geq 144 \text{ ms}$), a suppression was ob-

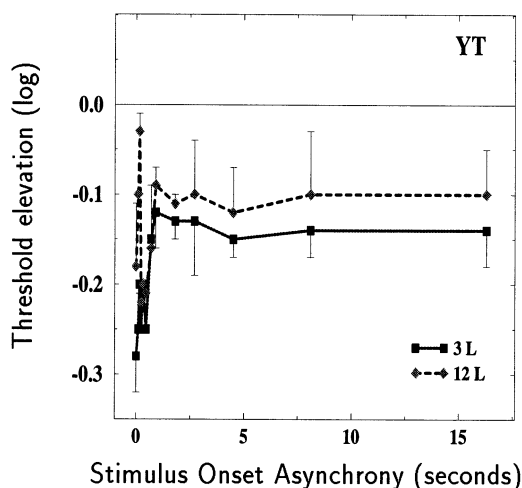


Fig. 4. Threshold elevation as a function of SOA for observer YT. Long-lasting facilitation was observed with shorter (3λ) and longer (12λ) distances. Isolated target threshold was $A_1 = 0.12I_0$ at SOA = 0. Error bars show 1 S.E.M. of differences between masking and corresponding control conditions. Each threshold estimate is based on three measurements.

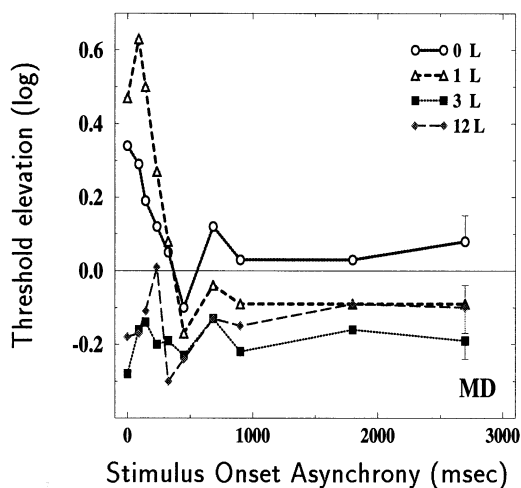


Fig. 5. Threshold elevation as a function of SOA for observer MD. Shorter distances (0λ and 1λ) were tested in addition to the longer distances (3λ and 12λ). Note that high-contrast masks at the target position (0λ) did not produce a significant long-term trace. Isolated target threshold was $A_1 = 0.07I_0$ at SOA = 0. Error bars show 1 S.E.M. of differences between masking and corresponding control conditions. Each threshold estimate is based on three measurements.

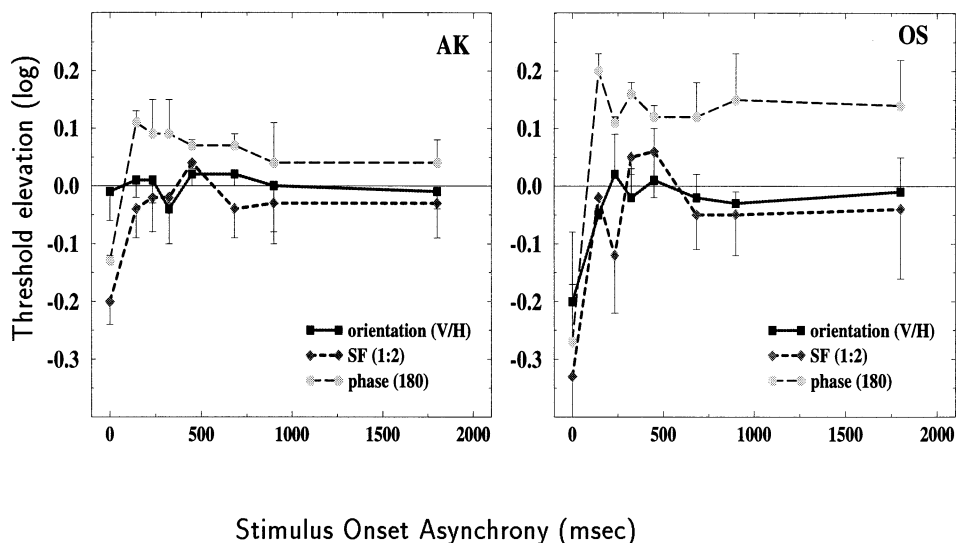


Fig. 6. Threshold elevation as a function of SOA for two observers (AK, OS). Mask GSs (distance 3λ) were varied either (1) in orientation, (2) in spatial frequency, or (3) in contrast phase. Isolated target threshold at SOA = 0 was $A_t = 0.05I_0$ for AK and $A_t = 0.13I_0$ for OS. Error bars show 1 S.E.M. of differences between masking and corresponding control conditions. Each threshold estimate is based on three measurements.

served, which lasted until 1800 ms of SOA (Fig. 6), presumably because of mask offset signals (see Section 4). This indicates that the masking effect is phase specific.

3.3. Monoptic/dichoptic experiment

In this experiment, mask (prime) and target were presented either to the same eye (i.e. mask to the left, target to the left) or to different eyes (i.e. mask to the left, target to the right). Masking and control conditions were compared within the same SOA. When they were presented to the same eye (monoptic masking condition), thresholds decreased after 300 ms of SOA compared with the monoptic control condition, whereas when they were presented to different eyes (dichoptic masking condition), threshold reduction did not occur compared with the dichoptic control condition (Fig. 7). These results indicate that the masking effect is monocular.

3.4. Global-configuration dependence

The wide range of the masking effect in space (12λ) and in time (16 s) indicates global characteristics, suggesting that it is affected by global spatial configurations [13,29]. To determine whether the masking effect depends on global configuration, an additional experiment was carried out. The target was always located foveally, but in one condition, the upper and the lower masks, of the 12λ configuration, were shifted 4λ to the left and 4λ to the right, respectively (a distance yielded to 12.6λ from the target). The target was located within the area defined by two masks (with local to global

orientation difference of 18.4°). In the other condition, both masks were shifted to the right by 4λ (both distances 12.6λ from the target). Results showed that the threshold decreased when the target GS was located 'within the area', whereas no significant effect relative to control level was observed when the target GS was located 'out of the area', indicating that the masking effect is global configuration-dependent (Fig. 8).

4. Discussion

The purpose of this study was to investigate the relationship between perception and memory by using a Gabor forward masking paradigm. By evaluating the time course of delayed detection thresholds, we found contrast detection facilitation lasting for the whole time range tested, up to 16 s. This temporal persistence was by far longer than perceptual integration times found in visual masking and in contrast summation studies [18–21,30], where SOAs larger than 300 ms did not show any interaction.

We found that thresholds depend on target delay relative to cue, both in the control and in the masking condition. In each case, the minimum threshold occurs at around 300 ms delay. Interestingly, the time course of the threshold decrease coincides with that of various temporal attention effects, such as inhibition of return (starting from around 300 ms of SOA) [25,31], attention blink (maximal effects obtained around 180–270 ms of SOA) [26], attention blindness (starting from about 250 ms of SOA) [32], and the negative priming effect (obtained around 200 ms after stimulus presentation) [33,34]. This suggests some relationship between tempo-

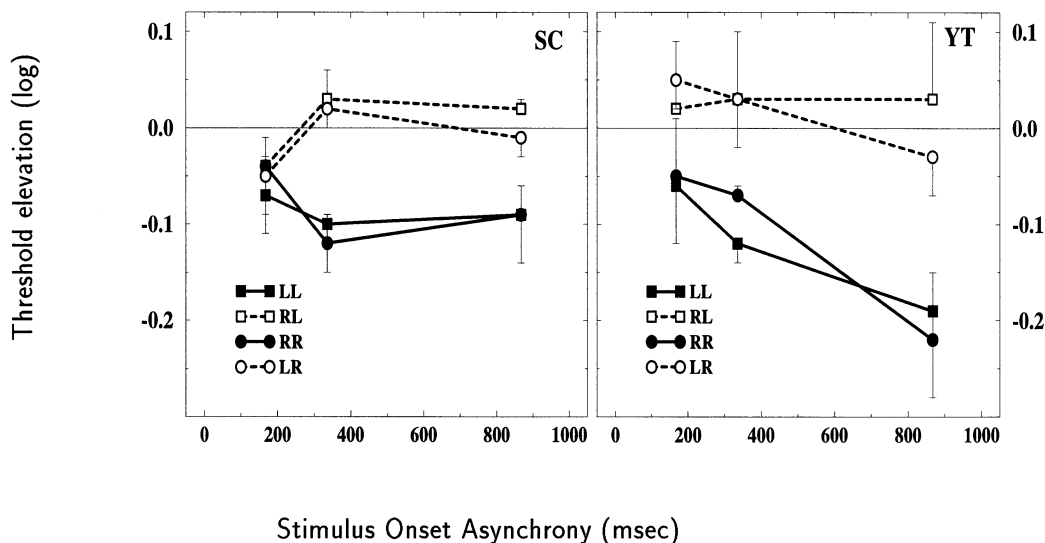


Fig. 7. Threshold elevation as a function of SOA for two observers (SC, YT). Continuous and dotted lines represent conditions with mask and target presented to the same and different eye, respectively (LR: mask to the left, target to the right eye, etc.). Facilitation was observed only when the delayed target was presented to the same eye as the preceding masks. Isolated target thresholds were $A_t = 0.14I_0$ for the left eye, $A_t = 0.13I_0$ for the right eye for SC, and $A_t = 0.34I_0$ and $A_t = 0.41I_0$ for YT. Error bars show 1 S.E.M. of differences between masking and corresponding control conditions. Each threshold estimate is based on three measurements for SC and four measurements for YT.

ral attention and the delayed facilitation. Presumably a dynamic attention process, similar to the ‘shut-and-lock’ mechanism in detection [35,36] takes place at around a 300 ms delay, establishing a persisting memory trace.

The facilitation by Gabor signal primes was specific for orientation, spatial frequency, and the eye presented, in accordance with perception [12] and memory recall (imagery; [16]), pointing to a close interface between perception and visual memory [22,23,37]. With

regard to the phase specificity, perception and memory showed different characteristics: enhancement was observed at SOA = 0 ms with masks of opposite contrast phase to the target, which is consistent with Zenger and Sagi [27], while suppression was found at SOA = 144 ms (ISI = 54 ms), persisting up to 1800 ms of SOA. Assuming that a delay of 54 ms of ISI is within the offset response time of the prime GSs, it is possible to attribute the delayed suppression to the stimuli disappearance [21,38]. A similar phenomenon was observed in memory studies using mental imagery. Ishai and Sagi [39] measured GS contrast sensitivity while the observers were imaging GS flankers, following a detection task (in a preceding block of trials) with stimuli containing flankers. While detection facilitation was observed with flankers pairs of same and opposite phase as target, only the flankers with phase equal to that of the target yielded facilitation in the imagery task. The functional similarity between the memory structure identified here and the one identified in the imagery studies [16,39] may point to a common underlying structure operating on a relatively long time scale (seconds here, minutes when using imagery).

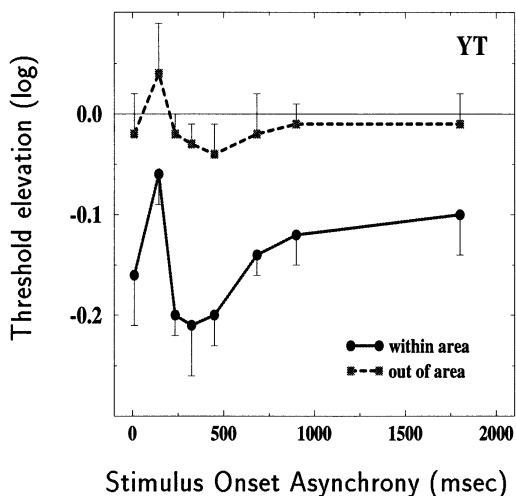


Fig. 8. Threshold elevation as a function of SOA (observer YT). Facilitation was observed only in the ‘within area’ condition, where the delayed target was located in between the two preceding masks. Isolated target threshold was $A_t = 0.09I_0$ at SOA = 0. Error bars show 1 S.E.M. of differences between masking and corresponding control conditions. Each threshold estimate is based on three measurements.

The present study extends previous findings concerning long-range facilitatory interactions [12] by adding the temporal dimension. The detection facilitation with delayed targets sometimes exceeds that observed with simultaneous presentation of mask and target, with maximal facilitation obtained at an SOA larger than zero. As these minima seem to depend on target-to-mask separation, an interesting relationship emerges between the temporal and the spatial dimensions. For the 3λ separation facilitation peaks at around 300 ms,

while for the 12λ separation facilitation peaks at around 800 ms. This result suggests that facilitation propagates in space [17] with a relatively slow velocity, reaching distant locations after some delay. Here, it takes about 500 ms to cross a distance of 1.35° , indicating a propagation speed of about $3^\circ/\text{s}$. Slow propagation is also consistent with the dynamics of perceptual organization ($10\text{--}20^\circ/\text{s}$) as revealed by grouping experiments [40], and with cortical dynamics ($10\text{--}20\text{ cm/s}$) as revealed by optical imaging methods [41]. The dependence on global configuration indicates that activity propagation may be anisotropic, propagating mainly along the axis defined by the orientation of the primes. This is in agreement with previous studies [13].

Surprisingly, primes at target location did not produce delayed facilitation. Using a target–prime distance of 0λ we found suppression that decayed slowly, reaching the control level at about 500 ms. It is possible that local inhibitory processes, operating at high contrast levels [7,27], act against the memory processes and/or do not generate memory traces. Indeed, using a low contrast prime at the target location we were able to measure long-lasting (16 s) detection facilitation [42]. This memory trace was also monocular, orientation and location specific, in agreement with the facilitation found here. Dependence on simple image features such as contrast (and orientation, eye) implicates the involvement of a low level memory structure, however, the functional properties are not necessarily different from those of structures underlying higher level priming effects, such as in recognition tasks [43].

To summarize, we found long-lasting, long-range facilitation of contrast detection, using a Gabor forward lateral masking paradigm. The facilitation persists for over 16 s. Facilitation strength depends on the global configuration of the stimuli (maximal for collinear target and masks), local parameters (orientation, spatial frequency, and phase), and the presented eye. These results suggest that spatial filters in low-level vision retain an input trace far beyond the perceptual integration times, indicating a mechanism of visual memory.

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References

- [1] Braddick O, Campbell FW, Atkinson J. Channels in vision: basic aspects. *Handbook of Sensory Physiology*. Vol III: Perception, 1978:3–38.
- [2] DeValois RL, DeValois KK. *Spatial Vision*. New York: Oxford University Press, 1990.
- [3] Campbell F, Robson J. Application of Fourier analysis to the visibility of gratings. *J Physiol Lond* 1968;197:551–66.
- [4] DeValois KK. Spatial frequency adaptation can enhance contrast sensitivity. *Vis Res* 1977;17:1057–65.
- [5] Blakemore C, Carpenter RHS, Georgeson MA. Lateral inhibition between orientation detectors in the human visual system. *Nature Lond* 1970;228:37–9.
- [6] Campbell FW, Kulikowski JJ. Orientational selectivity of the human visual system. *J Physiol Lond* 1966;187:437–45.
- [7] Cannon MW, Fullenkamp SC. Spatial interactions in apparent contrast: Inhibitory effects among gating patterns of different spatial frequencies, spatial positions, and presentations. *Vis Res* 1993;31:1985–98.
- [8] Chubb C, Sperling G, Solomon JA. Texture interactions determine perceived contrast. *Proc Natl Acad Sci USA* 1989;86:9631–5.
- [9] Ejima Y, Takahashi S. Apparent contrast of a sinusoidal grating in the simultaneous presence of peripheral gratings. *Vis Res* 1985;25:1223–32.
- [10] Sagi D, Hochstein S. Lateral inhibition between spatially adjacent spatial frequency channels? *Percept Psychophys* 1985;37:315–22.
- [11] Sagi D. Detection of an orientation singularity in Gabor textures: Effect of signal density and spatial frequency. *Vis Res* 1990;30:1377–88.
- [12] Polat U, Sagi D. Lateral interactions between spatial channels: Suppression and facilitation revealed by lateral masking experiments. *Vis Res* 1993;33:993–9.
- [13] Polat U, Sagi D. The architecture of perceptual spatial interactions. *Vis Res* 1994;34:73–8.
- [14] Kapadia MK, Ito M, Gilbert CD, Westheimer G. Improvement of visual sensitivity by changes in local context: Parallel studies in human observers and in V1 alert monkeys. *Neuron* 1995;15:843–56.
- [15] Polat U, Norcia AM. Neurophysiological evidence for contrast dependent long range facilitation and suppression in the human visual cortex. *Vis Res* 1996;36:2099–109.
- [16] Ishai A, Sagi D. Common mechanisms of visual imagery and perception. *Science* 1995;268:1772–4.
- [17] Polat U, Sagi D. Spatial interactions in human vision: from near to far via experience dependent cascades of connections. *Proc Natl Acad Sci USA* 1994;91:1206–9.
- [18] Breitmeyer BG. *Visual Masking: An Integrative Approach*. New York: Oxford University Press, 1984.
- [19] Foley JM, Boynton GM. Forward pattern masking and adaptation: Effects of duration, inter-stimulus interval, contrast, and spatial and temporal frequency. *Vis Res* 1993;33:959–80.
- [20] Georgeson MA, Georgeson JM. Facilitation and masking of briefly presented gratings: Time-course and contrast dependence. *Vis Res* 1987;27:369–79.
- [21] Watson AB, Nachmias J. Patterns of temporal interaction in the detection of gratings. *Vis Res* 1977;47:893–902.
- [22] Magnussen S, Greenlee MW, Asplund R, Dyrnis S. Stimulus-specific mechanisms of visual short-term memory. *Vis Res* 1991;31:1213–9.
- [23] Sperling G. The information available in brief visual presentations. *Psychol Monogr* 1960;74:1–29.
- [24] Squire LR. *Memory and Brain*. New York: Oxford University Press, 1987.

- [25] Posner MI, Cohen Y. Components of visual orienting. *Atten Perform* 1984;10:531–56.
- [26] Raymond JE, Shapiro KL, Arnell KM. Temporary suppression of visual processing in an RSVP task: An attentional blink? *J Exp Psychol: Hum Percep Perform* 1992;18:849–60.
- [27] Zenger B, Sagi D. Isolating excitatory and inhibitory non-linear spatial interactions involved in contrast detection. *Vis Res* 1996;36:2497–513.
- [28] Lawton BT, Tyler CW. On the role of X and simple cells in human contrast processing. *Vis Res* 1994;34:659–67.
- [29] Kovács I, Julesz B. A closed curve is much more than an incomplete one: Effect of closure in figure-ground segmentation. *Proc Natl Acad Sci USA* 1993;90:7495–7.
- [30] Foley JM. Human luminance pattern-vision mechanisms: Masking experiments require a new model. *J Opt Soc America A USA* 1994;1(1):1710–9.
- [31] Tanaka Y, Shimojo S. Location versus feature: Reaction time reveals dissociation between two visual functions. *Vis Res* 1996;36:2125–40.
- [32] Kanwisher NG. Repetition blindness: Type recognition without token individuation. *Cognition* 1987;27:117–43.
- [33] Tipper SP. The negative priming effect: Inhibitory effects of ignored primes. *Q J Exp Psychol* 1985;37:571–90.
- [34] Treisman A, DeSchepper B. Memory for novel visual stimuli. *Invest Ophthalmol Vis Sci (Suppl)* 1993;34:1288.
- [35] Broadbent DE, Broadbent MHP. From detection to identification: Response to multiple targets in rapid serial visual presentation. *Percept Psychophys* 1987;42:433–58.
- [36] Reeves A, Sperling G. Attention gating in short term visual memory. *Psychol Rev* 1986;93:180–206.
- [37] Regan D. Storage of spatial-frequency information and spatial-frequency discrimination. *J Opt Soc Am A USA* 1985;2:1619–21.
- [38] Tolhurst DJ. Sustained and transient channels in human vision. *Vis Res* 1975;15:1151–5.
- [39] Ishai A, Sagi D. Stimulus-specific short-term memory revealed by visual imagery. *J Cogn Neurosci* 1997;9:476–89.
- [40] Ben-Av MB, Sagi D. Perceptual grouping by similarity and proximity: Experimental results can be predicted by intensity autocorrelations. *Vis Res* 1995;35:853–66.
- [41] Grinvald A, Lieke E, Frostig RD, Hildesheim R. Cortical pointspread function and long-range interactions revealed by real-time optical imaging of macaque monkey primary visual cortex. *J Neurosci* 1994;14(5):2545–68.
- [42] Tanaka Y, Sagi D. A perceptual memory for low contrast visual signals. *Invest Ophthalmol Vis Sci (Suppl)* 1997;38:S963.
- [43] Ochsner KN, Chiu C-YP, Schacter DL. Varieties of priming. *Curr Opin Neurobiol* 1994;4:189–94.