



Attention and short-term memory in contrast detection

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Abstract

Low-contrast visual stimuli have been found to produce a memory trace, enhancing subsequent target detection for as much as 16 s. Here we show that the memory trace depends on dynamic interactions between low-level stimulus properties and a higher-level gating process. Detection of vertical targets (Gabor signals) was enhanced by preceding vertical Gabor primes, but suppressed by preceding tilted primes — pointing to a competitive process of dynamic resource allocation. The priming effect was also dependent on a temporal cue, activating a sensory gating process with maximal effect at 300–500 ms delay. The results suggest a two-step process in which attention affects transition between perception and memory: a non-selective gating process followed by competition between overlapping representations. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Visual memory refers to the retention of perceptual experience over various periods of time (i.e. < 0.5 s for iconic memory (Sperling, 1960; Hogben and DiLollo, 1974; Phillips, 1974), seconds for visual short-term memory (STM) (Phillips, 1974; Squire, 1987), minutes for working memory (Baddeley, 1986), and days for perceptual priming (Squire, 1987; Ochsner, Chiu & Schacter, 1994; Wiggs & Martin, 1998)). Of particular interest is its low-level structure in the visual processing stream (Regan, 1985; Magnussen, Greenlee, Asplund & Dyrnis, 1991; Magnussen & Greenlee, 1992; Magnussen, Greenlee & Thomas, 1996). Recently, we reported evidence for a perceptual memory for low-contrast visual signals (Tanaka & Sagi, 1998a,b). In our paradigm, contrast-modulated, spatially-localized sinusoidal gratings (*Gabor signals*, GSs) preceded similar target GSs with a temporal delay (*Gabor priming*). Long-lasting detection facilitation of GS targets was found with preceding low-contrast (at threshold) GSs, persisting for 16 s. This is far beyond visual integration time (Breitmeyer, 1984; Georgeson & Georgeson, 1987)

or iconic memory range (Sperling, 1960; Hogben & DiLollo, 1974). The facilitation was highly specific to visual features such as location, orientation, spatial frequency, and eye (Tanaka & Sagi, 1998b), yet phase insensitive (Tanaka & Sagi, 1998a, but see Tanaka & Sagi, 1998b), suggesting visual memory at early filtering stages in low-level vision. Moreover, the facilitation was masked with high-contrast GS interference, demonstrating that the memory is very sensitive to luminance contrast (Tanaka & Sagi, 1998a). These findings suggest that low-contrast perceptual signals can generate a long-lasting memory trace in early stages of the visual system, probably within the primary visual cortex.

Although a large body of studies addresses low-level temporal interaction between filters, using visual masking (Breitmeyer, 1984; Georgeson & Georgeson, 1987), sub-threshold summation (Watson & Nachmias, 1977), visual persistence (Hogben & DiLollo, 1974) or contrast adaptation (Greenlee & Heitger, 1988), the mechanisms involved in memory generation are not known. Visual masking, sub-threshold summation, and visual persistence all disappear within a few hundred ms (Hogben & DiLollo, 1974; Watson & Nachmias, 1977; Breitmeyer, 1984), while visual memory persists for a few seconds after stimulus presentation (Regan, 1985; Magnussen et al., 1991; Magnussen & Greenlee, 1992; Magnussen et al., 1996), up to 5 min when active recall

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(imagery) is used (Ishai & Sagi, 1995). Taken together with the evidence for longer term effects described above, and assuming these memory effects are a result of perceptual experience, there seems to be a phenomenological gap in the time course of visual processing. Here we look for some probe on processes linking perception and memory. More specifically, we ask whether memory generation requires, in addition to perceptual activity, a top-down control (a high-level ‘touch’). Gating processes (opening and closing a gate for memory generation) are assumed to take place in perceptual learning (Karni & Sagi, 1995), however, little is known about their role in short-term memory generation. Baddeley (1986) proposed a visual working memory, incorporating an attention-driven executive process, to link perception and memory. Sakai and Miyashita (1993) argued that attention may influence early visual processing and affect memory at the encoding stage. Reeves and Sperling (1986) hypothesized that attention gates memory access in digit identification during rapid-visual-serial-presentation (RSVP) task. It is not clear whether the ‘attention’ assumed to be involved in memory generation shares any mechanism with the ‘attention’ assumed to take part in object binding (Treisman & Galade, 1980), in computations of spatial relations (Julesz, 1981) or in detection facilitation by spatial or temporal cueing (Posner, 1980; Eimer, 1994). Here, we focus on the latter. It is known that visual detection is facilitated when a warning signal precedes the target by about 400 ms (Posner & Boies, 1971). As this temporal cueing effect occupies the time window of 300–500 ms after visual stimulation, tailing the sensory integration window and leading short-term visual memory, it seems to serve as a good candidate to bridge perception and memory.

The goal of this study is to determine (1) whether attention (by temporal cueing) affects early vision, namely contrast detection, and if so, (2) whether temporal cueing is critical to the generation of memory traces in low level vision. To demonstrate these (a) the time course of temporal cueing was investigated using temporally cued Gabor targets in contrast detection tasks, with and without temporal uncertainty, and (b) Gabor primes were added to test dependency of memory traces on prime to target timing.

2. Methods

2.1. Display

Stimuli were presented as grey level modulation on a Philips 17A color monitor, 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 38 cd/m^2 . Stimu-

lus 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 and mixed/fixed SOA experiments, stimuli were presented on a Sony GDM2000-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. In the dichoptic/monoptic experiments, stimuli were viewed with CrystalEyes E-1 stereo glasses with optic shutters that alternate in 120 Hz synchrony with the monitor, reducing the effective display luminance to 7 cd/m^2 . An 8-bit RGB mode was used, and Gamma correction was applied to produce linear behavior of the displayed luminance. The viewing distance was 100 cm.

2.2. Stimuli

A stimulus sequence consisted of a GS prime (*prime-interval*), followed after some delay by a GS target (*target-interval*) at the same central location (Fig. 1). The delay was defined as stimulus onset asynchrony (SOA, the time between prime and target onsets). The luminance distribution of a GS is computed by the equation

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

with x and y being the horizontal and vertical coordinates, respectively, and $T(t | t_0, du)$ a temporal square pulse. The spatial location of GS is determined by x_0 and y_0 , initial time at GS presentation by t_0 ($= 0$), its duration by du , its orientation by θ (in radians), and its wavelength by λ . The standard deviation of the Gaussian envelope is given by σ . For the basic stimuli used in the experiment, the spatial frequency of GSs (ω) = 6.7 cpd and $\sigma = 0.15^\circ$ (visual angle) were kept constant. θ was chosen from $0, 15, 45, 60$ and 90° for the GS prime and fixed at 0° (vertical orientation) for the GS target. Stimulus intensity distribution was defined by

$$I(x, y, t) = I_0 + A_{GS} GS_\theta(x, y, t)$$

with $A_{GS} = 0$ in uniform luminance intervals $A_{GS} = A_p \geq 0$ in prime-intervals and $A_{GS} = A_t \geq 0$ in target-intervals, and I_0 mean luminance (38 or 7 cd/m^2). Transition between intervals followed a temporal step function. Contrast is defined here as A_{GS}/I_0 . Each prime and target interval included two high-contrast peripheral crosses to minimize temporal uncertainty (Fig. 1), the size being $0.46^\circ \times 0.46^\circ$ each, the luminance being

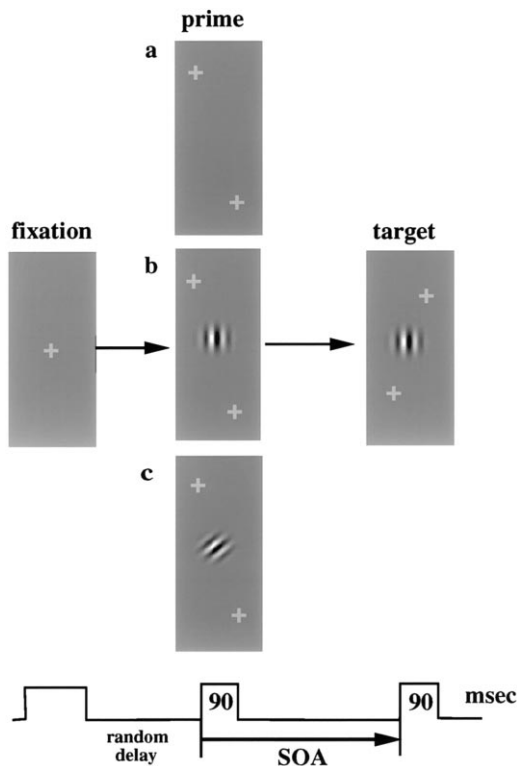


Fig. 1. Sample stimulus sequences: Prime and target displays contained two peripheral crosses (size and distances are not in scale in this figure). (a) No GS prime is presented, only crosses serving as temporal cues (control condition). (b) A foveal GS prime, followed by a GS target at the same foveal location. Prime and target orientations are identical (both 0°). (c) Prime orientation is different from target orientation (here 45°). On each trial, two sequences were presented with only one of them containing the target. The observer's task was to indicate which sequence (first or second) contained the target (2AFC). Different SOAs were tested in different sessions.

90 cd/m^2 (high contrast), located randomly in the area between 1.7° and 0.85° from the GS target, aligned at a direction of $\theta = -45^\circ$ but of $\theta = 45^\circ$ in prime displays. When there was no GSs presented in the prime interval, the crosses served as a temporal cue.

2.3. Experimental procedure

Two experimental conditions were tested: (1) the priming condition, in which GS primes in addition to peripheral crosses were presented prior to the GS target, (2) the control condition, in which GS primes were not presented and only peripheral crosses were presented in the prime interval (Fig. 1). The high-contrast peripheral crosses were presented to test whether there is a general temporal-cueing effect without GS primes. 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, the observer pressed a key to activate the trial sequence: a uniform luminance interval (450–900 ms, randomized), a first

prime-interval (90 ms) a uniform luminance interval (= SOA-90 ms), a first target-interval (90 ms), a uniform luminance interval (1710–2160 ms, randomized), a second prime-interval (90 ms), a uniform luminance interval (= SOA - 90 ms), a second target-interval (90 ms). In the *priming condition*, both of prime-intervals contained a GS prime but only one target-interval contained a GS target. In the *control condition*, GS primes were not presented ($A_p = 0$) and only peripheral crosses were presented during the prime-interval. Crosses were also presented in target-intervals. When SOA = 0, prime- and target-intervals overlapped for 90 ms, therefore prime served as a *pedestal* (Breitmeyer, 1984; Georgeson & Georgeson, 1987). All displays were viewed binocularly. In the monoptic and dichoptic experiments, the non-stimulated eye viewed the average luminance display (I_0), but the fixation was viewed binocularly to minimize fixation errors. High-contrast crosses, marking prime or target intervals, were presented only to primed and targeted eyes, respectively. Inter-trial-interval (ITI, an interval between the second target and the fixation in the next trial) was at least 3 s or more, depending on observer's reaction time.

Contrast thresholds for GS targets were measured using a temporal two-alternative forced choice (2AFC) procedure. The observers were asked to determine which of the two target-intervals contained the GS target (detection task). Auditory feedback, by means of a keyboard bell, was given immediately after an erroneous 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 sequence 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. The initial target amplitude (A_t) was set at about 1.5 times the control threshold contrast, attempting to minimize effects from previous blocks (Tanaka & Sagi, 1998a). In several experiments, threshold elevation was computed relative to the detection threshold of the GS target in the absence of the GS prime at the same SOA (*control*, prime amplitude $A_p = 0$).

A session, consisting of groups of blocks, lasted approximately 1 h. Each block contained about 60 trials. The following three major experiments were carried out, where different parameters were manipulated separately. (1) Temporal-cueing/GS priming experiment, where temporal delay, eye dependency, orientation specificity, and contrast modulation were tested independently. Different SOAs were tested (0, 90, 180, 270, 360, 450, 540, 630, 720, 900 and 1800 ms). Different GS-prime orientations (0 and 45°) and control conditions (no GS-primes) composed a group of triple

blocks. In which only one SOA was tested. SOA was fixed across trials within the block, except in the *temporal uncertainty experiment* described below. The order between priming and control conditions was randomized within each triple block. SOAs were increased gradually from shorter to longer. Different eyes and longer SOAs (5400, 10800 ms) were tested in the monoptic/dichoptic experiments. To test orientation/contrast dependency, different GS-prime orientations (0, 15, 45, 60 and 90°) and different GS-prime contrasts (from 0 (control) to high-contrast (0.5)) were tested in separate blocks. The same orientations were tested in the same session. GS-prime contrast was increased from lower to higher in each block. (2) Independent temporal-cueing experiment, where the effect of temporal cueing was independently examined with a temporal separation of non-GS cues, SOA was fixed within the block. (3) Temporal uncertainty experiment, where SOAs were randomly chosen between 0, 500, and 900 ms for each trial. Throughout the experiments, each datum point was repeated at least three times. Seven observers (MD, CVC, IO, BC, RO, GM, and one of the authors, YT) participated in the experiments. The observers were college/high-school students (age 17–26 years), who did not know the purpose of the experiments except for the first author. MD, CVC, and YT had experienced the priming paradigm before.

3. Results

3.1. Temporal-cueing/GS priming experiment

In the Gabor priming paradigm, a stimulus sequence consisted of GS primes, followed by GS targets after a temporal delay (SOA). Detection thresholds for the GS targets were plotted as a function of SOA to examine the time course of priming effects.

3.1.1. Temporal dependency

Temporal dependency of the priming effect is shown for an SOA range between SOA = 0 (prime and target overlapped in time) to SOA = 1800 ms. Both control and two prime-orientation conditions (0° = *identical* and 45° = *tilted* prime) were tested (Fig. 1). Prime contrast was set at the threshold level for each observer. Fig. 2 shows the results of four observers. At SOA = 0, threshold was reduced with identical prime orientations (0.17 ± 0.01 logarithmic units; mean \pm SE, $P < 0.001$, $n = 4$ observers; paired t -test) and slightly reduced with tilted orientations (0.08 ± 0.03 log units, $P > 0.05$, ns), possibly due to sub-threshold summation with overlapping receptive fields. When cueing signals preceded targets, thresholds were dramatically reduced for *all conditions* (control, identical-, and tilted-prime) at SOA of 360–540 ms relative to thresholds at SOA = 0. Ob-

server IO showed decreased performance at SOA of 90–180 ms, possibly due to masking effects from signal offsets (Tanaka & Sagi, 1998b), but still showed threshold reduction at 360–540 ms SOA for all conditions. The largest facilitation (threshold reduction) was observed with SOA around 500 ms for all observers. The magnitude of maximal facilitation relative to SOA = 0 was 0.19 ± 0.01 log units ($P < 0.001$, $n = 4$ observers, paired t -test) for the control, 0.16 ± 0.01 log units ($P < 0.001$) for GS primes identical to GS target, and 0.08 ± 0.01 log units ($P < 0.005$) for tilted GS primes. This effect can be attributed to general *temporal-cueing effects* (or warning signals by timing) (Posner & Boies, 1971), since threshold reduction was observed in both priming and control conditions. Larger SOAs (> 630 ms) yielded baseline (SOA = 0) performance in the control condition. The presence of low-contrast GS prime with identical orientation yielded threshold reduction of 0.20 ± 0.02 log units ($P < 0.005$, $n = 4$ observers, paired t -test) relative to control at the same SOAs (> 630 ms). The threshold reduction was observed with SOA as large as 1800 ms. When GS prime orientation was tilted by 45°, thresholds, at larger SOA (> 630 ms), *increased* relative to control by 0.12 ± 0.01 log units ($P < 0.005$, $n = 4$ observers, paired t -test). This long-term suppression points to an inhibitory component of the memory trace. Note that at longer (1–2 s SOAs, target thresholds differ by a factor of 2.1 (0.32 log units) between identical and tilted prime orientations.

3.1.2. Eye dependency

Eye dependency was tested in the monoptic/dichoptic experiments with GS prime and target presented either to the same or different eyes. Prime contrast was set at the threshold level for each observer and each eye (Section 2). Facilitation was observed (Fig. 3) in both monoptic and dichoptic conditions during the first 240–480 ms either with or without GS primes. Data are presented in Fig. 3 for two observers, BC (maximal facilitation, control: 0.24 ± 0.07 , monoptic; 0.23 ± 0.07 , dichoptic; 0.008 ± 0.097 , difference between monoptic and dichoptic, all $n = 4$ at SOA = 480 ms) and YT (maximal facilitation, control: 0.24 ± 0.12 , monoptic; 0.13 ± 0.08 , dichoptic; 0.12 ± 0.14 , difference between monoptic and dichoptic; all $n = 5$ at SOA = 360 ms). This result indicates that temporal cueing affects both monocular and binocular processes in the same manner.

Only the monoptic prime condition yielded long-lasting threshold reduction, in agreement with previous results (Tanaka & Sagi, 1998a,b). Here, for observer BC, facilitation was observed up to 10.8 s with a magnitude of 0.25 ± 0.03 log units ($P < 0.005$, $n = 15$ at SOA > 700 ms, paired t -test; Fig. 3, top). Observer YT was tested in detail with shorter SOAs (< 1 s), with

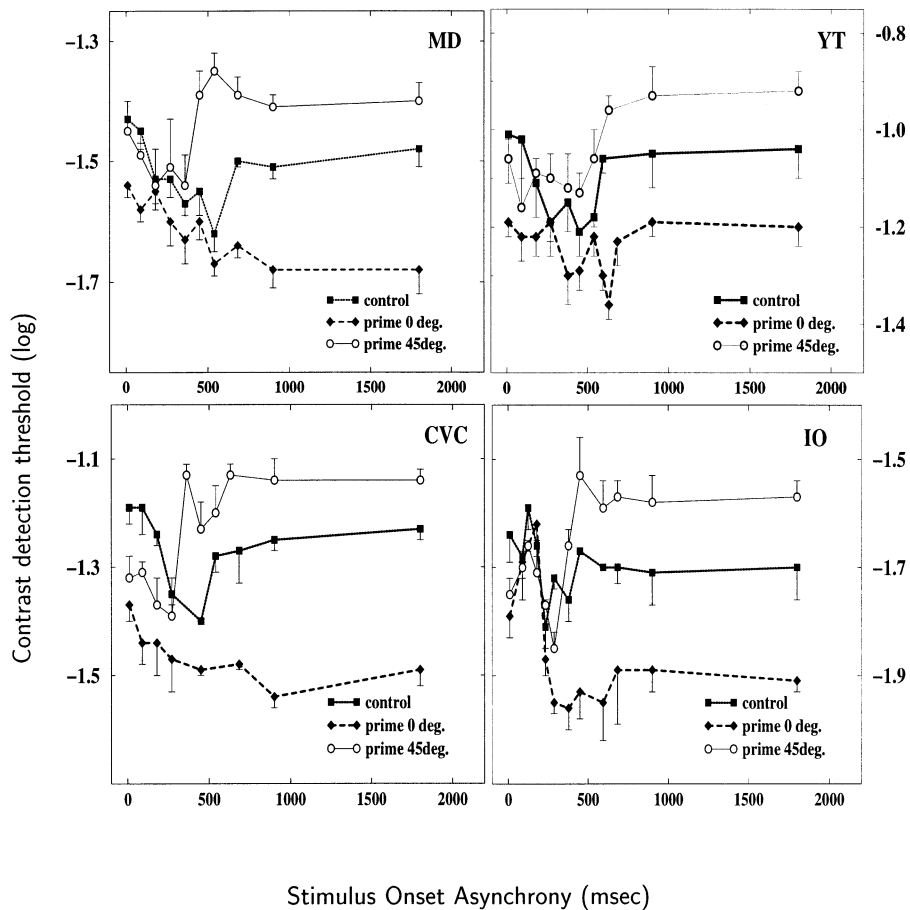


Fig. 2. Time course of detection facilitation and suppression. Dependence of contrast detection threshold on prime-to-target asynchrony (SOA) for control (no GS prime), prime orientations 0 and 45° (observers MD, YT, CVC, IO). In these and succeeding graphs, each datum point shows an average value of three or more measurements unless described otherwise, and error brackets indicate one standard error of mean (SEM). Threshold reduced during the first 360–540 ms for all conditions. Threshold facilitation is preserved with 0° primes at longer SOAs, while threshold suppression can be seen with 45° primes at longer delays. GS-prime contrasts, A_p : MD, $0.05I_0$; YT, $0.08I_0$; CVC, $0.05I_0$; IO, $0.05I_0$, for both orientations.

facilitation (prime orientation at 0°: 0.17 ± 0.02 log units, $P < 0.005$, $n = 8$ at $SOA > 700$ ms, paired t -test; Fig. 3 bottom) and suppression (prime at 45°: 0.17 ± 0.06 log units, $P < 0.05$, $n = 8$ at $SOA > 700$ ms, paired t -test) observed only in the monocular condition. Dichoptic conditions did not show long term effects (BC: 0.03 ± 0.03 , $n = 20$; YT 0°: 0.01 ± 0.04 , $n = 8$; YT 45°: 0.02 ± 0.04 , $n = 8$ all at $SOA > 700$ ms), demonstrating *monocular* inhibitory/facilitatory memory traces (as for monocular–binocular relationship, see Section 4).

3.1.3. Contrast and orientation dependency

To assess contrast modulation together with orientation specificity of the long-lasting effect, different GS-prime contrasts were tested with different orientations. SOA was fixed at 900 ms, about six times longer than the duration of classical temporal summation (Watson & Nachmias, 1977; Breitmeyer, 1984), thus well within the range of visual short-term memory (Phillips, 1974; Tanaka & Sagi, 1998a,b; Wiggs &

Martin, 1998). Detection threshold decreased (facilitation) with GS-prime contrast around threshold, when GS-prime and target orientations were identical (both 0°, Fig. 4), in accordance with our previous study (Tanaka & Sagi, 1998a). Threshold increased (suppression) at around threshold prime contrast when GS prime was tilted by 15–60°. Suppression disappeared (paired t -test; 0.01 ± 0.004 log units, $P > 0.10$, $n = 4$ observers, at threshold) when GS-prime orientation was orthogonal (90°).

Both facilitation and suppression were found to depend on GS-prime contrast. Low-contrast GS-primes (around threshold) yielded maximal facilitation (paired t -test: 0.25 ± 0.04 log units, $P < 0.01$, four observers) and maximal suppression (0.22 ± 0.02 log units, $P < 0.005$, four observers) (Fig. 4). When prime contrast was three to four times above threshold, both facilitation and suppression disappeared. These results indicate that memory facilitation and suppression depend on both orientation *and* contrast, exhibiting a 0.47 log-unit full range effect on sensitivity.

3.2. Independent temporal-cueing experiment

To demonstrate that the general facilitation with SOA around 500 ms is directly associated with the memory generation process, temporal-cueing signals (peripheral crosses) were separated in time from GS primes, so that temporal-cueing effects could be tested independently of GS-priming effects. First, peripheral crosses were presented for 90 ms, serving as a pure temporal cue, then after a delay, a GS prime was presented for 90 ms (CPA, cue-prime asynchrony; Fig. 5). A GS target was presented after another interval

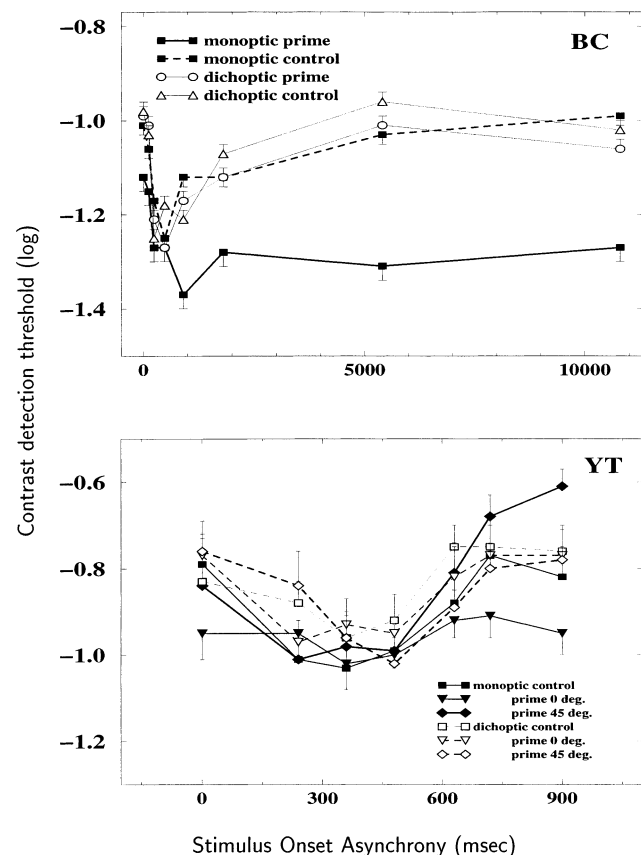


Fig. 3. Time course of detection facilitation and suppression. Top panel: Thresholds are shown for observer BC as a function of longer SOAs (up to 10.8 s), for monoptic and dichoptic prime/control conditions. GS-prime orientation was 0° . Each datum point is the average of four or more measurements with the same eyes (prime-target: left–left, right–right) in the monoptic condition, and different eyes (left–right, right–left) in the dichoptic condition. Threshold reduced during the first 240–480 ms for all conditions (independent of eye), however, only the monoptic prime condition yielded long-lasting (10.8 s) facilitation. GS-prime contrast, A_p : $0.10I_0$. Bottom panel: Orientation dependency (GS primes, 0 or 45° , observer YT) for monoptic and dichoptic priming/control conditions. Each datum point is the average of four or more measurements. Thresholds reduced with SOA 240–480 ms independent of orientation and eye, increasing to baseline level (SOA = 0) at longer SOAs for all dichoptic conditions and for the monoptic control condition. Memory facilitation (with 0° primes) and suppression (with 45° primes) were observed only for the monoptic prime condition with SOA > 700 ms. GS-prime contrast, A_p : $0.10I_0$ for both orientations.

(PTA; prime-target asynchrony). The interval between the temporal cue and the GS targets was fixed at 900 ms and different intervals between temporal-cue and GS prime (CPA) were tested (Fig. 5, CPA = 900-PTA). Baseline threshold was measured without GS primes, with cue to target asynchrony (CTA) fixed at 900 ms.

Threshold elevation relative to baseline was plotted as a function of PTA for three observers in Fig. 6. Different prime orientations (0 , 15 and 45°) were tested in separate sessions. Threshold reduction was observed with PTA at 0 ms depending on orientation (0.20 ± 0.03 log units, $P < 0.025$ for 0° , $n = 3$ observers; 0.13 ± 0.02 log units for 45° , observer MD, $n = 3$ repetitions; 0.07 ± 0.04 log units for 15° , $n = 2$ observers, $P > 0.20$, ns; paired t -test). This facilitation was gradually reduced or disappeared with PTA around 180–450 ms depending on orientation and observers. These results possibly reflect a sensory integration process studied in the masking literature (Watson & Nachmias, 1977; Breitmeyer, 1984).

Threshold enhancement appeared again (0.23 ± 0.04 log units, $P < 0.05$, three observers: paired t -test) with PTA at 500–600 ms for all prime orientations. This enhancement effect remained with PTA at 700–900 ms for GS primes with identical orientation (0.20 ± 0.04 log units, $P < 0.05$, $n = 3$ observers; paired t -test), while threshold suppression was observed (0.16 ± 0.02 log units, $P < 0.025$, $n = 3$ observers; paired t -test) for tilted (15 or 45°) GS primes. Interestingly, priming effects with PTA at 500–600 ms (corresponding to cue-prime delay of 300–400 ms) were 60% higher than with simultaneous cue and GS-prime presentations, suggesting that pattern (GS) priming is most efficient when attention (called by the preceding temporal cue) is allocated to the prime.

Based on the data presented in Fig. 6, the PTA 900 ms range can be divided into three parts: *Perceptual integration* (0–300 ms), *attention* (300–700 ms), and *memory* (700–900 ms). Perceptual integration reflects facilitation depending on orientation differences, attention effects are independent of orientation, while memory seems to reflect competition between different orientations. These strongly suggest that temporal attention is critical to memory generation.

3.3. Temporal uncertainty experiment

If specific timing signals, such as temporal cueing (i.e. ‘automatic alerting’, Posner & Boies, 1971), are critical to establish a memory trace, then one would expect that memory would not be generated when timing information is not provided. To demonstrate this hypothesis, experiments were conducted where the observers were faced with temporal uncertainty regarding prime target intervals; each block of trials included three SOA intervals (SOAs; 0, 500 and 900 ms), one of which was

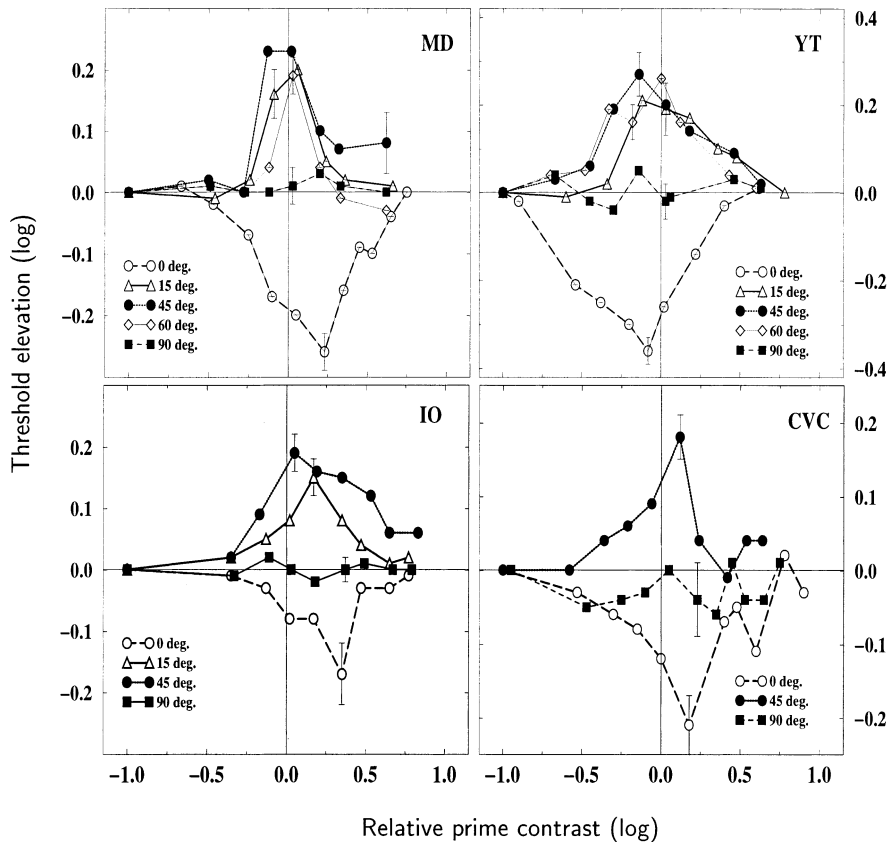


Fig. 4. Orientation and contrast dependence of detection. Contrast detection threshold (relative to control, in logarithmic units) as a function of GS-prime contrast (relative to GS-prime threshold, in logarithmic units) are shown for four observers (MD, YT, IO, CVC) with SOA fixed at 900 ms. Five GS-prime orientations (0, 15, 45, 60 and 90°) were tested in different sessions, while GS-target orientation was kept at 0°. Maximal enhancement and suppression were obtained when GS-prime contrast was close to its threshold, independent of individual sensitivity. GS-target thresholds A_t : Subject [0, 15, 45, 60 and 90°] = MD[0.05 I_0 , 0.04 I_0 , 0.05 I_0 , 0.05 I_0 , 0.05 I_0], YT[0.08 I_0 , 0.09 I_0 , 0.08 I_0 , 0.07 I_0 , 0.07 I_0], IO[0.03 I_0 , 0.03 I_0 , 0.02 I_0 , -, 0.03 I_0] CVC[0.05 I_0 , -, 0.06 I_0 , -, 0.05 I_0]. GS-prime contrast was equal to target threshold contrast ($A_p = A_t$).

randomly selected on each trial. Thus, observers could not adapt to a specific time course. Both control and priming conditions were tested with temporal uncertainty (mixed SOA condition). The different temporal conditions (certainty and uncertainty) were tested in different sessions. Two prime orientations (0 and 45°) were tested, in addition to the control condition.

The experimental results (see Fig. 7) show that temporal uncertainty abolished the detection facilitation (temporal cueing) at SOA = 500 ms relative to SOA = 0, for all cue-prime conditions, effectively reversing the effect (control: -0.02 ± 0.003 log-units, $P < 0.025$; 0°: -0.11 ± 0.01 log-units, $P < 0.025$; 45°: -0.07 ± 0.003 log-units, $P < 0.005$; $n = 3$ observers, paired t -test). Of particular interest is the absence of a measurable detection facilitation by the 500 ms temporal cue in the absence of pre-trial temporal information (temporal uncertainty: -0.02 log units, see above, as compared with temporal certainty: 0.19 ± 0.02 log-units, $n = 3$ observers, $P < 0.01$, paired t -test). This indicates that the process triggered by the temporal cue needs to be tuned to the temporal requirements of the task.

With primes added to the temporal cue, the temporal behavior of the priming effect is somewhat more complicated (see Fig. 2), and primed detection facilitation at 500 ms was absent, or reduced (Fig. 7, fixed prime relative to control, 0°: 0.10 ± 0.02 log-units, $P < 0.025$; 45°: 0.04 ± 0.01 log-units, $P > 0.05$; while in uncertainty condition. 0°: 0.03 ± 0.01 log-units, $P > 0.05$; 45°: 0.02 ± 0.01 log-units, $P > 0.05$; $n = 3$ observers, paired t -test).

Of importance here is the dependency of memory trace at 900 ms on temporal uncertainty. Inspection of Fig. 7 shows a significant memory effect in the fixed SOA condition. Detection was improved relative to control with same orientation prime (0°: 0.20 ± 0.01 log-units, $P < 0.001$, $n = 3$ observers, paired t -test), and was reduced with the different orientation prime (45°: -0.12 ± 0.01 log-units, $P < 0.001$, $n = 3$ observers, paired t -test). However, both long term facilitation and suppression disappeared in the uncertainty condition (0°: 0.03 ± 0.01 log-units, $P > 0.10$; 45°: 0.01 ± 0.01 log-units, $P > 0.20$, $n = 3$ observers, paired t -test).

Threshold reduction at SOA = 0 (contrast discrimination) was less affected by uncertainty. Facilitation for

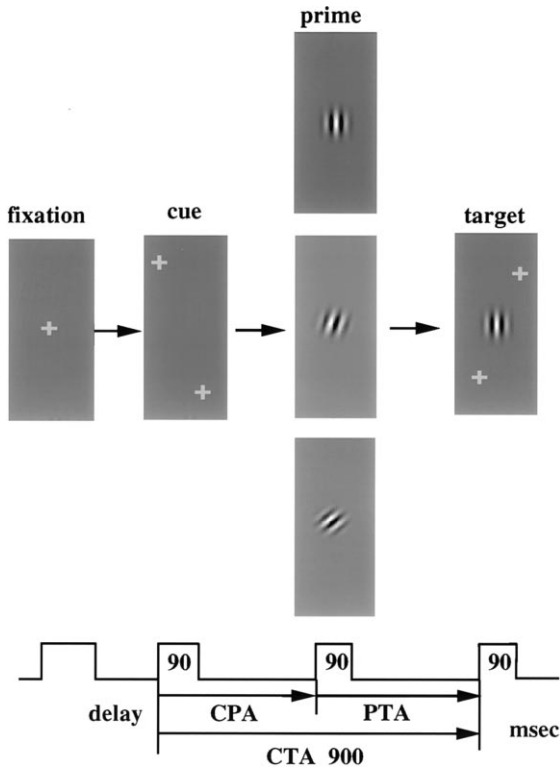


Fig. 5. Stimulus used to separate temporal cues from GS-orientation cue. A target preceded by an independent temporal cue (two crosses) and a GS prime in succession. GS-prime orientation was either 0, 15 or 45° with GS-target orientation kept at 0°. Different CPA/PTAs were tested in different sessions.

both orientations remained despite the temporal uncertainty (paired *t*-test; 0.11 ± 0.02 log-units, $P < 0.025$ for 0°, 0.08 ± 0.01 log-units, $P < 0.025$ for 45°). At SOA =

0, the results with temporal uncertainty are slightly reduced relative to the temporal certainty condition (0.11 versus 0.17 and 0.08 versus 0.12 log-units for 0 and 45° primes, respectively), with differences reaching statistical significance (certainty versus uncertainty at SOA = 0, paired *t*-test, 0°: 0.06 ± 0.01 log-units, $P < 0.05$; 45°: 0.04 ± 0.01 log-units, $P < 0.05$, $n = 3$ observers).

The results presented here indicate that some time dependent (tuned) process is required to activate temporal-cueing effects, and to produce inhibitory/facilitatory memory traces, while perceptual facilitation (pedestal effects at SOA = 0), probably depending on sensory integration, takes place automatically.

4. Discussion

Contrast detection was found to be facilitated when target followed a temporal cue by 300–500 ms. This time dependency is in agreement with previous results from visual-alertness or arousal studies in attention psychophysics (Posner & Boies, 1971; Hübner & Hafter, 1995) and neurophysiology (Eimer, 1994; Marrocco, Witte & Davidson, 1994). Our results showed that the detection enhancement by temporal cueing transferred between eyes and disappeared with longer time delays (more than 900 ms) or when the quality of temporal information was reduced by increasing temporal uncertainty. We further showed that the combination of temporal cueing with low-contrast pattern priming can produce long-term effects on detection.

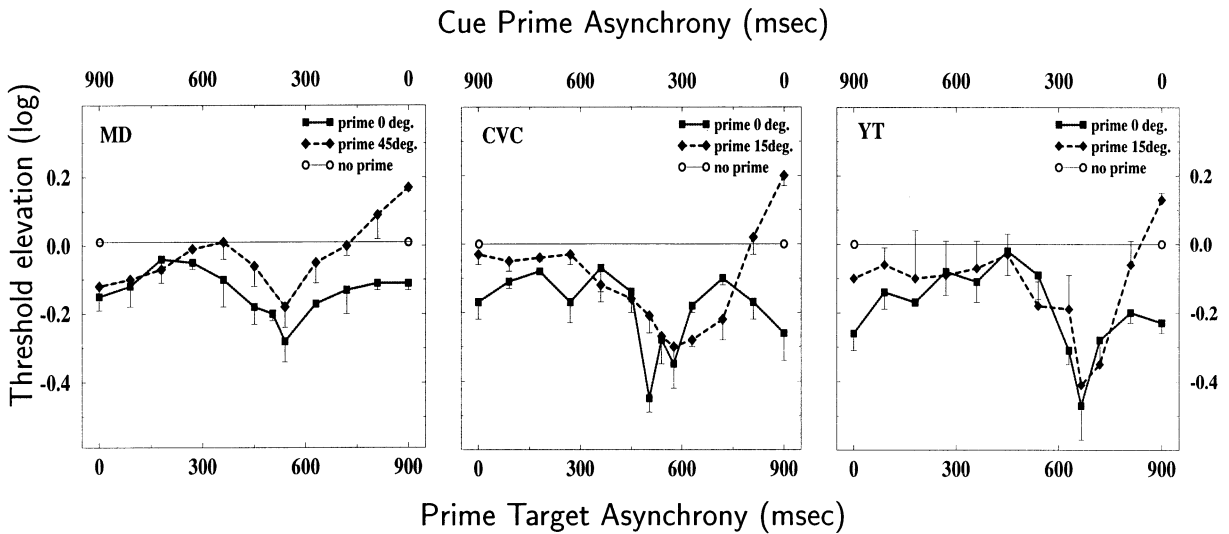


Fig. 6. Separating temporal cue and pattern priming. Dependence of detection threshold on prime-to-target time (PTA) while cue-to-target asynchrony (CTA) is fixed at 900 ms. Threshold elevation relative to control is shown as a function of PTA for three observers (MD, CVC, YT). An initial threshold reduction (PTA = 0) decreased or disappeared (PTA < 300 ms), however larger threshold reduction was observed with PTA at 500–600 ms, with facilitation persisting at PTA of 900 ms. These imply separated processes of perceptual integration, attention, and memory, respectively (see text). GS-target thresholds at SOA 900 ms, A_t : MD, $0.05I_0$; CVC, $0.04I_0$; YT, $0.08I_0$. GS-prime contrasts, A_p : MD, $0.05I_0$; CVC, $0.05I_0$; YT, $0.10I_0$ for each orientation.

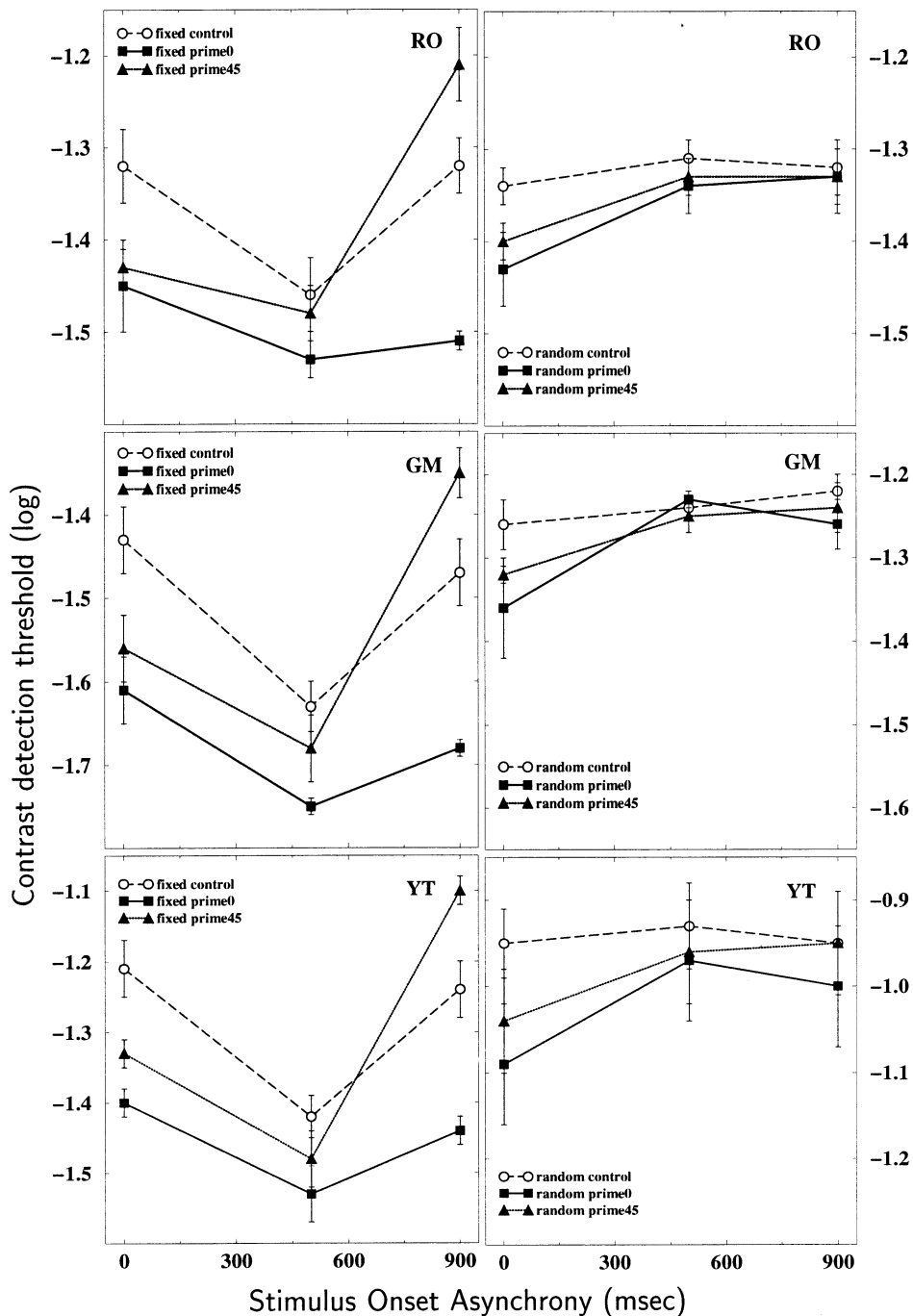


Fig. 7. Effects of temporal uncertainty. Threshold is shown for three observers (RO, GM, YT) as a function of SOA for control (no GS-primes, left column) and two priming conditions (GS-prime orientations: 0 and 45 right column). In the fixed SOA condition, thresholds reduced with SOA 500 ms in both prime/control conditions, yielding primed facilitation (0° or suppression (45°) at 900 ms of SOA. In the mixed SOA condition, threshold reduction at SOA 500 ms disappeared for both GS-prime orientations as well as memory facilitation/suppression at SOA 900 ms, while perceptual facilitation (SOA = 0) for both GS-prime orientations remained. GS-prime contrasts, A_p : RO, $0.04I_0$; GM, $0.04I_0$; YT, $0.07I_0$ for each orientation.

These effects can be facilitatory, when prime orientation equals target orientation, or suppressive, when orientations differ by 30–60° with delayed detection thresholds showing a 2-fold change in threshold between these two conditions. Unlike the pure temporal cueing effects, pattern priming, though requir-

ing temporal information, was found only when prime and target were presented to the same eye. The results point to a low-level anatomical site for these long-term memory traces, with memory generation dependent on higher level time-locked processes.

Our results point to the existence of monocular memory traces which depend on processes at binocular level of processing (i.e. temporal cueing). It seems that temporal cueing opens a time-limited window of attention which facilitates, or enables, monocular processes originating from both eyes. However, only active monocular tracks are affected by the binocular processes to produce priming effects. Thus, memory traces are generated by an interaction between top-down binocular signals and bottom-up monocular signals at early levels of visual processing. It is possible that global top-down processes (attention), originating at higher cortical areas, *gate* (i.e. enable or disable) local bottom-up signals in the visual cortex, generating memory traces. A possible anatomical substrate for this interaction to take place is a neuronal network in which monocular inputs from both eyes converge. The gating hypothesis is in accordance with Reeves and Sperling's (1986) *attentional gating* model, where a hypothetical temporal 'window' *gates* visual information into short-term memory. Reeves and Sperling also find a 500 ms delay for the temporal window. Cortical facilitation within a similar time window after temporal cueing was also observed in recent studies using steady-state visual evoked potential (Müller, Teder-Salejarvi & Hillyard, 1999). Note that temporal cueing is effective only within a limited time window (around 500 ms), thus cannot be accounted for by reduced temporal uncertainty only.

Our results show orientation dependent priming effects. Long-term facilitation was observed with equal orientation primes and long-term suppression was observed with primes tilted relative to target. These effects developed over time, as no suppression was observed with synchronous prime and target. An orientation difference of 45° produced some facilitation with zero delay but suppression with long delays. This points to a network dynamics where cross-orientation inhibition (between adjacent orientations) develops within 200–300 ms. While cross-orientation inhibition was suggested for refined orientation tuning (Blakemore, Carpenter & Georgeson, 1970) and contrast gain control (Heeger, 1992) and indicated in contrast masking psychophysics (Zenger & Sagi, 1996), our results point to the critical role of top-down control over the orientation-network dynamics. Similar cross-orientation dynamics, but on a faster time scale (100 ms) and without attentional manipulations, was observed in the primary visual cortex of anesthetized macaques (Ringach, Hawken & Shapley, 1997) pointing to a possible anatomical substrate of the network. Our finding of the critical role of temporal cueing for the delayed inhibition is consistent with recent psychophysical results suggesting that attention activates winner-take-all competition among visual filters (Lee, Itti, Koch & Braun, 1999). The attentional lateral-inhibitory network dy-

namics may reflect a process of *resource allocation*, where one orientation is selected among others (competition), a process in line with the neural selection model (Desimone & Duncan, 1995; Desimone, 1996) developed to account for object selection in higher visual processing stages (i.e. inferotemporal and prefrontal cortices) within the delayed matching-to-sample paradigm (Miller, Li & Desimone, 1993; Miller, Eriksen & Desimone, 1996). Our data suggest that a similar competition process takes place in earlier visual processing stages as well. Evidences for attentional effects in primary visual cortex are reviewed in Posner and Gilbert (1999).

Facilitation and suppression were contrast specific, observed only when prime contrast was low, with the peak sensitivity narrowly tuned around prime threshold. While it is not obvious why this should happen, this result is consistent with previous reports concerning intensity dependence of visual persistence (Hogben & DiLollo, 1974), probably pointing to some adaptation process operating at higher contrast levels. However, *contrast adaptation*, manifested as increased sensitivity after high-contrast stimulation, probably has little effect here as stimulus durations are too short (90 ms) for contrast adaptation to take effect. Note also that negative traces (sensitivity reduction) were not observed with high-contrast primes, indicating that memory generation is a process not directly related to contrast adaptation. As our results show that memory generation depends on an efficient stimulus processing within a slow temporal window of attention (around 500 ms), it is possible that these temporal interactions are not optimally effective during high-contrast stimulation (e.g. fast high contrast response < 200 ms, with slow attention allocation > 200 ms). This hypothesis is supported by recent results showing existence of memory traces after high-contrast stimulation under conditions where attention is optimally allocated to the *high-contrast* prime, with temporal cue preceding prime (by 500 ms, Tanaka & Sagi, 1999). Facilitation and suppression may also depend on filter tuning properties such as orientation bandwidth and size, which are contrast dependent. Spatial integration by receptive fields of primary visual cortex (V1) was found over larger extents with low contrast stimulation as compared with high-contrast stimulation (Sceniak, Ringach, Hawken & Shapley, 1999). Memory traces may be affected by dynamic changes in visual receptive fields (Pettet & Gilbert, 1992; Das & Gilbert, 1995) with low contrast primes triggering an increased receptive field selectivity for basic visual features such as orientation, possibly involving receptive field expansion, enhancing primed orientation sensitivity while reducing sensitivity to other orientations within the initial orientation bandwidth (45°) (Ringach et al., 1997; Lee et al., 1999) without affecting the orthogonal orientation. High-con-

trast stimulation would on this account, reset receptive fields parameters.

The facilitation and suppression caused by near-threshold prime signals may be related to positive/negative object priming effects (Tipper, 1985; DeSchepper & Treisman, 1996; etc). In Tipper's studies two different overlapping stimuli (line drawings) were presented and subjects were asked to attend one of them. After a delay, either attended or unattended stimuli were presented. Naming responses were faster with attended stimuli (positive priming) but slower with unattended stimuli (negative priming). Using Tipper's paradigm, DeSchepper and Treisman (1996) showed that complex stimuli without familiar cues can have a negative priming effect if not attended, lasting as long as a month. Our results show *positive* priming with identical prime orientations and *negative* priming with tilted orientations, even though observers were not asked to attend the primes. Note that the stimuli used in our study have more primitive visual features (single GSs) as compared with Tipper's stimuli (complex drawings). It is possible that different types of attention are operating. Both in Tipper (1985) and DeSchepper and Treisman's (1996) studies, attention was called for the visual objects voluntarily and explicitly, suggesting the involvement of some higher-level processes. In our study, attention was drawn by temporal cueing, which reduced temporal uncertainty. This suggests that attention can affect various stages of the visual processing stream in a different manner, generating different types of visual memory.

Overall, this study showed that early visual processing operates in a very dynamic and plastic manner, leading to visual memory. Presumably, the low-level feature-selective processes and high-level attention processes interact within a limited time window (500 ms delay) at limited loci in the brain (the primary visual cortex), generating perceptual memory.

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