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A perceptual memory for low-contrast visual signals

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ABSTRACT **Detection of a visual signal can be facilitated by simultaneous presentation of a similar subthreshold signal. Here we show that the facilitatory effect of a subthreshold signal can persist for more than 16 s. Presenting a near-threshold Gabor signal (prime) produced a phase-independent increase in contrast sensitivity (40%) to similar successive signals (target) for a period of up to 16 s. This effect was obtained only when both prime and target were presented to the same eye. We further show that the memory trace is inactivated by presenting high-contrast signals before the target. These results suggest that activated neurons in the primary visual cortex retain a near-threshold memory trace that persists until reactivated.**

Visual stimuli may generate memory traces persisting over different time scales. Of particular interest is the time scale over which a low-level image description is preserved. Visual persistence or iconic memory refers to the retention of perceptual experience, which can be recalled if not masked within a very short period of time (<0.5 s) (1–4). Visual short-term memory, persisting for seconds, was demonstrated in visual discrimination tasks in humans for image features such as spatial frequency (5, 6), orientation (7), and direction of motion (8). Exposure to a visual stimulus also has a persisting effect on sensory detection related to receding visual targets, without the observer consciously recalling the first (prime) stimulus—a phenomenon termed repetition priming (9). Priming of visual objects appears to be supported by a perceptual representation system that preserves information about the three-dimensional structure of objects at a presemantic level (10). Although different neuronal mechanisms may subserve repetition priming and short-term memory (11–13), behaviorally both phenomena can be manifested in improved (enhanced) perception on repetition. Active retrieval of visual memory demonstrates the persistence of low-level visual information such as luminance contrast, as the detection of a visual target can be facilitated for a few minutes when human observers recall (using mental imagery) previously perceived stimuli (14). These findings suggest that visual memory can be generated during the persistence of a low-level "iconic" trace. Here, we investigate visual memory traces of briefly presented stimuli by examining sensitivity to a delayed visual stimulation. Our measure was contrast sensitivity for fovealy located grating targets [Gabor signals (GSs) (15)], with each target preceded by a similar GS serving as a prime.

METHODS

In our procedure, a stimulus sequence consisted of a prime GS (prime interval) followed after some delay by a target GS (target interval) at the same central location [Fig. 1*A*. Stimulus onset asynchrony (SOA), defined as the time between prime and target onsets; $GS(x, y) = \cos(\omega x)\exp(-(x^2 + y^2)/\sigma^2)$, ω = 6.7 cycles per degree (cpd), σ = 0.15°, stimulus intensity distribution $I(x, y) = I_0 + A_{GS}GS(x, y)$, 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; transition between intervals followed a temporal step function. Contrast is defined here as A_{GS}/I_0]. Contrast thresholds for the targets were measured by using a temporal two-alternative forced choice procedure. Each trial consisted of two stimuli sequences, only one of which had a target. Before each trial, a fixation cross (0.32° × 0.32°, 90 cd/m^2) was presented at the center of the screen. When ready, the observer pressed a key to activate the trial sequence (Fig. 1*A*): 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), or a second target interval (90 ms). Both prime intervals contained a GS prime, but only one target interval contained a target GS. In control experiments, primes were not presented ($A_p = 0$), and both prime intervals assumed uniform luminance. Each prime and target display contained two high-contrast crosses located in the periphery to minimize temporal uncertainty (0.46° × 0.46° each, at 3.4° distance from the prime and at 1.7° distance from the target). All displays were viewed binocularly. In the monoptic and dichoptic experiments, the nonstimulated eye viewed the average luminance display, 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. The inter-trial interval (an interval between the second target and the fixation in the next trial) was at least 3 s or more, depending on the observer's response time.

The observers were asked to determine which of the two target intervals contained the target GS (the detection task). Auditory feedback, by means of a keyboard bell, was given immediately after an erroneous response. The target contrast threshold was determined by using a staircase method, in which target amplitude (A_t) was increased by 0.1 log unit in trials after an erroneous response and decreased by 0.1 log unit after 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. Threshold elevation was computed relative to the detection threshold of the target GS in the absence of the prime GS at the same SOA (control, prime amplitude $A_p = 0$).

Each session (about eight blocks of trials) lasted approximately 1 h. The luminance contrast of the prime GS and the SOA were varied between blocks of trials, but were fixed within each block of trials. Observers (n = 7, including Y.T.) were seated in a dark environment in front of a raster monitor with a mean screen luminance of $I_0 = 40\ cd/m^2$, using natural pupils.

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Abbreviations: GS, Gabor signal; SOA, stimulus onset asynchrony; cpd, cycles per degree.

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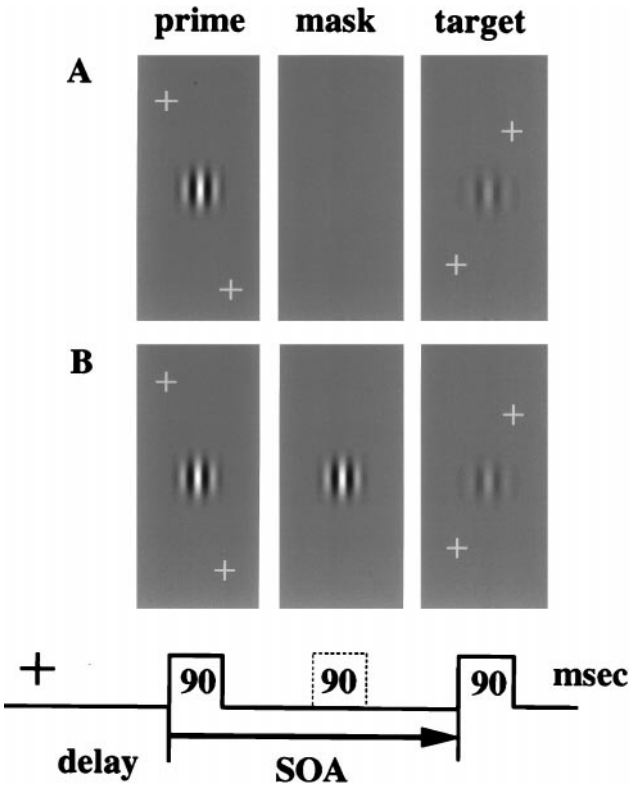

FIG. 1. Sample stimulus sequences: (*A*) A foveal prime GS (prime interval) followed by a target GS (target interval) presented at the same foveal location. (*B*) A target GS preceded by both a prime and a mask GS. Prime and target displays contained two peripheral crosses (size and distances are not in scale in this figure). 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.

The area of uniform luminance, viewed from a distance of 125 cm, extended 9.6° × 9.6° [Philips Brilliance 17A, (Philips, Eindhoven, the Netherlands) controlled by an ADAGE 3000 raster display system with 3 × 10 bits DACs, 512 × 512 screen resolution at 60 Hz refresh rate]. In dichoptic experiments, viewing distance was 100 cm and illuminated area extended 9.56° × 6.72° [Sony GDM2000TC (Sony, Tokyo), controlled by Silicon Graphics REALITY-ENGINE with 3 × 8 bits digital–analog converters; CrystalEyes E-1 stereo glasses (Sterographics, San Rafael, CA) with optic shutters at 120 Hz, 1280 × 450 screen resolution].

RESULTS

Contrast detection thresholds for target GSs were measured as a function of prime GS contrast with SOA set to 900 ms, about 6 times longer than known sensory integration time (16). Thresholds relative to control are depicted in Fig. 2*A*, showing a maximal detection enhancement with prime contrast at or near threshold. The magnitude of maximal threshold reduction was 0.25 ± 0.01 (mean ± SE, $n = 3$ observers) in log units (44% increase of sensitivity). High-contrast primes did not affect contrast detection thresholds relative to control. As prime contrast increased beyond the point of maximum enhancement, the target threshold increased steeply toward control. This increase indicates that the effect is very sensitive to prime contrast. Since the SOA used was within the time range of visual adaptation, where high-contrast stimuli viewed for a few minutes generate a reduced sensitivity, we considered the possibility that the memory trace is a result of luminance persistence rather than of contrast *per se*. Tests were carried out with target and prime having opposite contrast polarity (a 180° phase shift), showing a phase-independent enhanced sensitivity (Fig. 2*B*; maximal enhancement with same polarity, 0.21 ± 0.01 and with opposite polarity, 0.19 ± 0.02, mean ± SE, $n = 2$ observers, SOA = 900 ms).

To determine the temporal extent of the memory trace, we carried out experiments using different SOA values (0–16,290 ms), with prime contrast set at its optimal value (5% and 38% above prime contrast detection threshold for observers YT and SC, respectively). In addition, we tested for interocular transfer of the prime effect. When prime and target GSs were presented to the same eye, enhancement was observed: 0.33 log units with simultaneous presentation of prime and target (SOA = 0 ms), followed by absence of enhancement with 200–315 ms of SOA (see also ref. 17). Enhancement reappeared after 540 ms of SOA and persisted until the maximal SOA used, 16,290 ms (Fig. 3). Facilitation was not observed when prime and target GS were presented to different eyes, indicating that the effect is monocular, in agreement with previous measurements at SOA = 0 (18). Similar results (19) were obtained when the low-contrast prime GS was replaced by two high-contrast, co-oriented and co-axial GS flankers (20). Note that enhancement is observed at an SOA more than 100 times longer than typical perceptual integration times observed before in suprathreshold masking experiments (16) and in subthreshold summation (both "prime" and target to be detected) (21). The absence of long-term effects in the previous studies can be attributed to their use of high-contrast mask and/or limited range of SOA used.

To compare the magnitude of the memory trace with perception, we conducted a contrast discrimination experiment (SOA = 0 ms; i.e., prime serving as a contrast pedestal). In these experiments, observers were asked to discriminate between two GS of slightly different contrast (using a two-alternative forced-choice method with a staircase to estimate contrast discrimination thresholds; see *Methods*). The result was a typical just noticeable difference curve (18, 22), where the discrimination threshold improved by the presence of a pedestal GS at near-threshold contrast (Fig. 4, maximal enhancement: 0.33 and 0.3 log unit for observers CVC and YT, respectively, as compared with 0.17 and 0.22 at SOA = 900 ms), and deteriorated as a power function with increasing pedestal contrast. Data from contrast discrimination (SOA = 0) and primed detection (SOA = 900 ms) experiments are depicted in Fig. 4, with observers CVC and YT replicating the primed detection data presented in Fig. 2 (here, $\omega = 6.7$ cpd, $\sigma = 0.15°$, target duration = prime duration = 90 ms). Note that, at the subthreshold region, both threshold curves decrease with increasing pedestal/prime contrast, but the primed detection curves are shifted to the right by about 0.5 log unit (×3.16), indicating that about 32% of the input prime contrast is effective at 810 ms after prime disappearance. [Suprathreshold prime contrasts produce facilitatory traces of smaller magnitudes, possibly because of their inhibitory effects (22) and masking properties (Fig. 5). Also, it is possible that there are separate memory traces for enhanced (threshold) and suppressed (suprathreshold) neuronal activities, as suggested by the findings of Miller and Desimone (23) in inferotemporal cortex.]

To assess the selectivity of the memory trace for basic visual features, we manipulated the prime GS orientation, retinal location, and presented eye. Prime contrast was varied (within ±0.5 log unit around prime threshold) and SOA was set to 900 ms. Facilitation was found to be orientation-specific: when target and prime were orthogonal (vertical target preceded by horizontal prime), no enhancement was observed (maximal enhancement 0.02 ± 0.01, $n = 3$ observers). Facilitation was location-specific as well: when the prime GS ($\sigma = \omega^{-1} = 0.15°$) was shifted 0.45° of visual angle upwards from the target position, no enhancement was seen across various prime GS

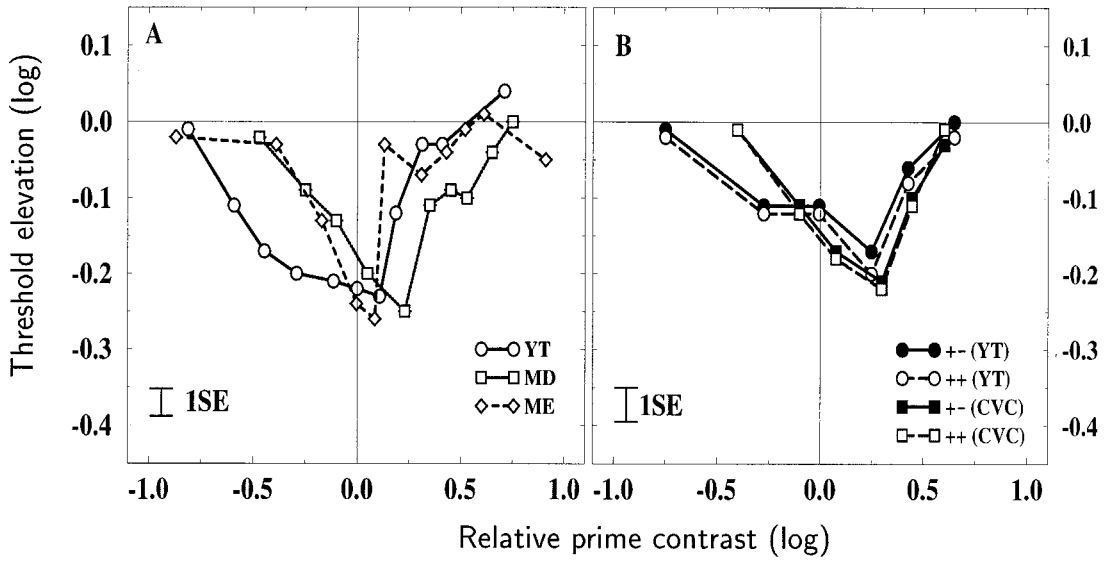

FIG. 2. Contrast detection threshold (relative to control, in log units) as a function of prime contrast (relative to prime threshold, in log units). Each datum point is the average of three or more measurements, with SOA = 900 ms. (*A*) Target and prime with the same GS parameters (three observers, here target interval duration was 36 ms, ω = 6.7 cpd, σ = 0.15°). (*B*) Data from experiments where trials with prime and target having the same and opposite polarity were mixed. Target detection threshold depends on prime contrast, reaching a minimum when prime contrast is about 38% above prime threshold. The effect is independent of the phase relationship between prime and target. In *B*, primes were of positive polarity on all trials, while targets of either positive or negative polarity were presented on different trials in random order, and GS assumed lower spatial frequencies (ω = 0.5 cpd, σ = 2°, target interval duration, 90 ms), to minimize phase effects because of small deviations of eye fixations. Note that maximal enhancement is obtained just above prime contrast threshold for all observers, independent of individual sensitivity. Target GS thresholds, A_t: MD, $0.08I_0$, ME, $0.06I_0$, YT, $0.18I_0$ in *A*, and CVC, $0.02I_0$, YT, $0.06I_0$ in *B*. Error bars show one standard error of the mean (SE).

contrasts (maximal enhancement 0.04 ± 0.02, n = 3 observers). Enhancement could be observed when using primes consisting of two supra-threshold GSs flanking the target location (19). Finally, facilitation was found to be monocular: threshold enhancement was found only when the same eye observed both prime and target, regardless of prime contrast (maximal enhancement for the various primed eye–target eye combinations: left–left 0.17 ± 0.02, right–right 0.16 ± 0.02, right–left 0.02 ± 0.01 and left–right 0.03 ± 0.01 log unit, mean ± SE, n = 3 observers).

One important property that distinguishes perceptual memory from more processed memories is its fragility to future visual stimulation (4, 6, 14, 24). We examined whether intervening stimuli during the prime-target delay interfere with the memory trace found here. Another high-contrast GS (mask GS: 30% contrast; otherwise the same orientation, spatial frequency, and size as target GS) was inserted between prime and target. The interstimulus interval was 810 ms between prime and mask and 810 ms between mask and target (Fig. 1*B*). Memory facilitation was greatly reduced with the mask GS (Fig. 5; maximal enhancement 0.02 ± 0.01 log unit, n = 2 observers), indicating that the memory trace can be inactivated by a high-contrast Gabor mask. We used this result to test for accumulation of facilitatory effects across trials. Tests were carried out with the high-contrast GS mask preceding the prime GS, thus probably clearing any facilitatory traces from

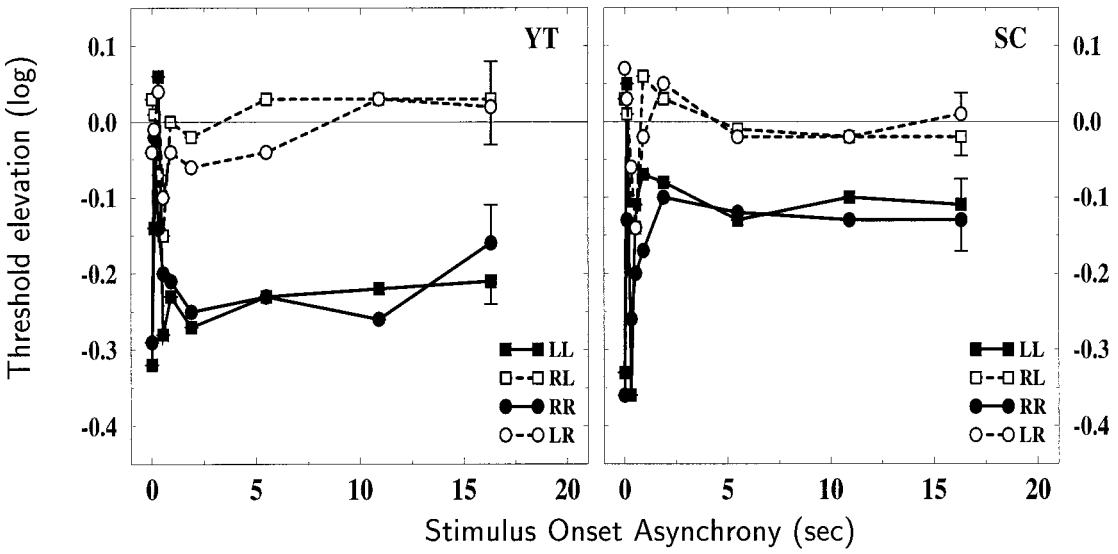

FIG. 3. Time course of contrast threshold enhancement. Threshold facilitation is shown as a function of SOA for two observers (YT and SC) for monoptic and dichoptic conditions (see *Methods*). Facilitation lasts for 16 s when target and prime are presented to the same eye, but not when presented to different eyes. Averaged monocular thresholds, A_t: YT, $0.19I_0$; SC, $0.07I_0$. Error bars show one standard error of mean (SE) of differences between prime and corresponding control with zero prime contrast (C_p = 0) threshold. LL, prime and target to left eye; RL, prime to right and target to left eye; RR, prime and target to right eye; LR, prime to left and target to right eye.

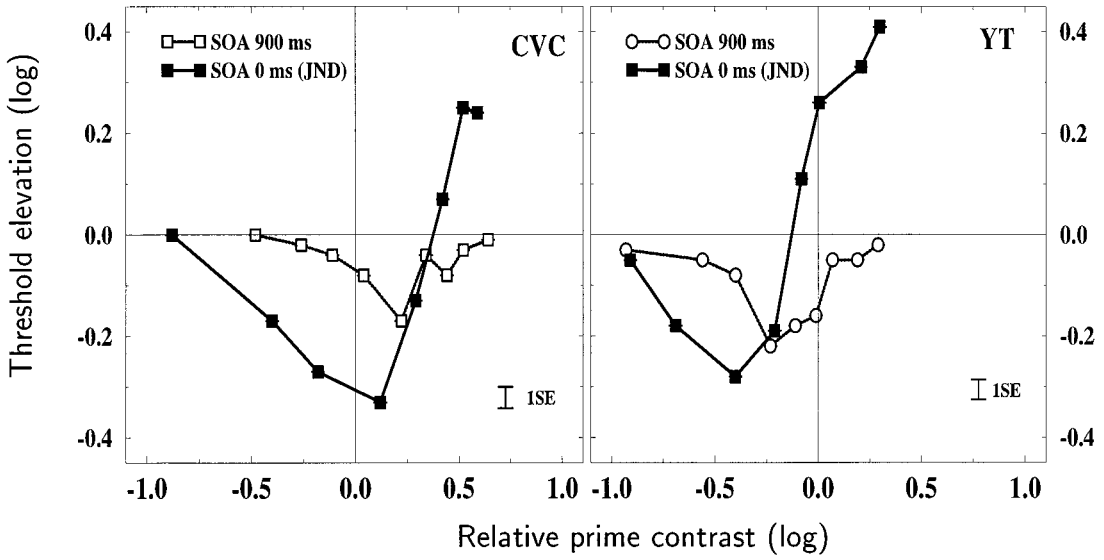

FIG. 4. Contrast discrimination (SOA = 0) compared with primed detection (SOA = 900 ms). Curves share similar properties when prime (or "pedestal" at SOA = 0; just noticeable difference) contrast is below contrast detection threshold. At this region, primed detection curves are shifted by about 0.5 log unit to the right, implying reduced sensitivity to prime at 900 ms relative to 0 ms by a factor of 3. Data presented for two observers with target GS thresholds, A_t: CVC, $0.04I_0$; YT, $0.13I_0$. Error bars show one standard error of the mean (SE) of differences between mask/prime and corresponding control threshold.

previous trials. Fig. 5 shows that in this condition enhancement occurred with prime contrast at threshold, similar in magnitude to that observed with the no-mask condition, although with a narrower tuning. This narrower tuning may indicate some long-term facilitatory effects in the absence of the preceding mask.

DISCUSSION

The main effect uncovered by use of the Gabor priming paradigm is the detection facilitation after presentation of a near-threshold GS. The facilitation was long-lasting (16 s), far more so than perceptual integration time (16) or visual persistence (3), and suggests the establishment of a memory trace whereby the prime GS exerts its effect on the perception of the subsequent test GS. The memory trace could be inactivated with a high-contrast mask GS and was contrast-dependent, pointing to a close interface with perception. A comparison between contrast discrimination data (SOA = 0) and primed detection data (SOA = 900 ms) showed a similar contrast dependency at low-pedestal/prime-contrast levels. Primed detection curves are shifted toward higher pedestal/prime contrasts, indicating reduced contrast effectiveness, yielding an effective contrast input of 32% at SOA = 900 ms, 810 ms after prime disappearance. It seems that low-contrast stimuli produce a significant long-lasting memory trace that is cleared only by the flow of high-contrast visual stimulation. As the trace is well localized within target size, but still phase insensitive, it may be related to an early stage of visual processing with limited spatial integration, such as the second

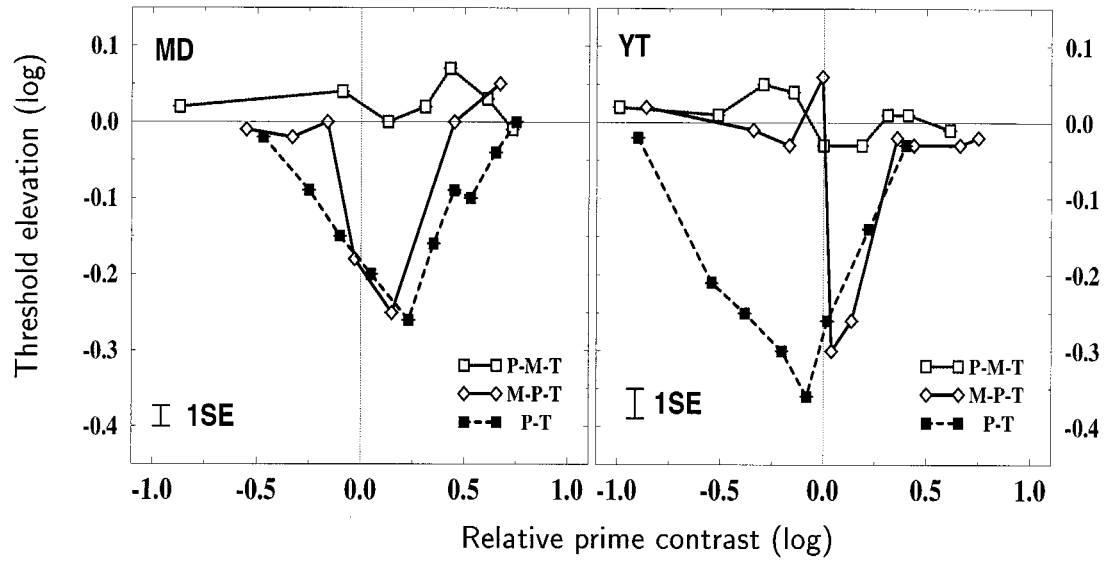

FIG. 5. Detection threshold relative to corresponding control is shown as a function of prime GS contrast with SOA = 1800 ms, with a mask GS inserted at SOA = 900 ms (see Fig. 1*B*, marked as P-M-T), and with a mask GS followed by prime GS (M-P-T), as compared with the single GS prime presentation (P-T) with SOA = 900 ms for two observers. Facilitation was blocked with the high-contrast intervening mask, whereas narrowly tuned facilitation was observed with the mask preceding the prime. Data presented for two observers with target GS thresholds, A_t: MD, $0.06I_0$, YT, $0.10I_0$. Error bars show one standard error of the mean (SE) of differences between prime and corresponding control threshold.

stage of spatial filtering described in ref. 22. Results from texture discrimination (25) and from lateral masking (26) studies point toward long-term plasticity in early cortical stages of visual processing. Indeed, the memory trace shares the same characteristics of feature selectivity found in perceptual learning, such as being eye-, orientation-, and location-specific (25, 26). In light of the neuronal response selectivity profile in the primary visual cortex of the primates (27), our results suggest that the memory trace can be subserved by and retained within the primary visual system, albeit in a fragile form. It is not clear yet under what conditions this trace can be consolidated, if at all.

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