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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 a simultaneous presentation of a similar sub-threshold signal. Here we show that this facilitatory effect persists for more than 16 seconds. Presenting a near-threshold Gabor signal (prime) produced a phase independent increase in contrast sensitivity (40%) to similar successive signals (target) for a period up to 16 seconds. This effect was only obtained when both prime and target were presented to the same eye. We further show that the memory trace can be destroyed by presenting high contrast signals. These results suggest that activated neurons in the primary visual system retain a near-threshold memory trace that persists until reactivated. This memory trace may subserve the consolidation process of perception into visual long-term memory.

INTRODUCTION

Visual short-term memory (STM) is a retention of perceptual experiences which last a short period of time [1, 2, 3]. For example, visual discrimination tasks in humans involve temporal retention of visual features such as spatial frequency [4, 5], orientation [6], and direction of motion [7]. 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 pre-semantic level [8]. Neuronal recordings in inferotemporal cortex (IT) of monkeys exhibit 'long-lasting' activities [9, 10, 11]. Active retrieval of visual memory (*imagery*) also demonstrates luminance contrast persistence: detection of a visual target can be facilitated for a few minutes when human observers 'imagine' previously perceived similar stimuli [12]. These findings suggest that visual memory can be generated during the persistence of 'iconic' trace. Here, we investigated visual STM generated by briefly presented stimuli by examining sensitivity to a delayed visual stimulation. A forward masking (priming) paradigm was used to analyze stimulus traces persisting for a few seconds.

METHODS

A prime Gabor Signal (GS) [13] was shown first (90 ms), followed by a target GS presentation at the same central location (Fig. 1 upper panel). The temporal delay (SOA: Stimulus Onset Asynchrony) between prime and target was set at 900 ms, which was about 6 times longer than that known to produce forward masking effects [14]. The task was to detect the target GS . Contrast detection thresholds for target GS were measured as a function of prime GS contrast. The luminance contrast of prime GS varied from 0 (no prime) to higher contrasts. Seven observers (including one of the authors, YT) participated in the experiments. A temporal two-alternative forced choice (2 AFC) procedure was used. Each trial consisted of two stimuli sequences, only one of which had a target. Before each trial, a small fixation cross ($0.32° \times 0.32°$, 90 cd/m^2) was presented at the center of the screen. When ready, the observer pressed a key activating the trial sequence; no-stimulus interval (450 to 900 ms, randomized), a first prime interval (90 ms), no stimulus interval (=SOA–90 ms), a first target interval (36 ms), no-stimulus interval (1710 to 2160 ms, randomized), a second prime interval (90 ms), no stimulus interval (=SOA–90 ms), a second target interval (36 ms). No-stimulus (uniform screen luminance of 40 cd/m^2) intervals were randomized to minimize temporal repetition effects. Each prime and target GS were accompanied by two peripheral crossings (0.46° x 0.46° each, at 3.4° distance from prime, and at 1.7° distance from the target), to minimize temporal uncertainty. The observer was asked to perform a detection task: to determine which of the two target intervals contained the target GS. Auditory feedback, by means of a keyboard bell, was given immediately after an erroneous response. Each session consisted of eight blocks, including the control. Target contrast threshold (between 7 to 15%) was determined by a staircase method [16]. Threshold elevation was computed relative to detection of the target GS in the absence of the prime GS (prime contrast = 0%).

RESULTS

Facilitation of the contrast detection threshold was observed when the prime GS contrast was at the near-threshold region (Fig. 2a). Interestingly, high prime contrasts did not facilitate target detection: optimal facilitation was found with near-threshold contrasts. The maximal facilitation was statistically significant. The average magnitude of maximal threshold enhancement was 0.23 ± 0.02 (mean±SE, n=4 observers) in logarithmic units (40% increase of sensitivity). The target threshold steeply increased towards control just after prime contrast crossed the absolute threshold, indicating the effect is very sensitive to the prime contrast.

To determine the temporal extent of the near-threshold facilitation, we manipulated the time delay between prime and target: SOA was altered from 0 (discrimination threshold) to 16,290 ms in different blocks of trials. Prime GS contrast was set just-above threshold level, where maximal facilitation was observed. When prime and target GSs were presented to the same eye, facilitation was observed; it started from the simultaneous presentation of prime and target (SOA=0 ms), followed by the absence of facilitation (with 200-315 ms of SOA. See also [19]). The facilitation *re*appeared after 540 ms of SOA, and persisted until the maximal SOA used, 16,290 ms (Fig. 3b). Facilitation disappeared when prime and target GS were presented to different eyes, indicating that the effect is monocular, in agreement with previous measurements at SOA=0 [17]. Note that facilitation is observed at an SOA more than 100 times longer than typical perceptual integration times observed before in suprathreshold masking experiments [14] and in subthreshold summation (both prime and target to be detected) [18]. As these long SOAs are 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 due to luminance persistence, rather than contrast per-se. Tests were carried out with target and prime having opposite contrast polarity (a 180° phase shift), showing a phase independent enhancement at SOA 900 ms (Fig. 2b; maximal enhancement of same, 0.22 ± 0.01, and opposite polarity, 0.21 ± 0.02, mean$\pm$SE, n=2 observers).

To compare the magnitude of memory with perception, we conducted a contrast discrimination task (SOA=0 ms; i.e., prime and target were overlapped) and obtained a typical Just Noticeable Difference (JND) curve [17], where discrimination threshold improved by the presence of a masking GS at near-threshold contrast (maximal enhancement: 0.28 and 0.4 log units for observers CVC and YT respectively, as compared with 0.17 and 0.27 at SOA=900 ms with the same stimulus parameters), and deteriorated as a power function [17, 16] with increasing mask contrast. The optimal mask contrast was the same as in the delayed-detection condition shown in Fig. 2a, suggesting that memory directly derives from perceptual processes. It can be shown that the internal response behaves as if 23% of the subthreshold input magnitude persisted for 900 ms*.

To assess the selectivity of the memory trace, we manipulated the prime GS orientation, retinal location, and presented eye. Facilitation was found to be orientation-specific: when target and prime were orthogonal (vertical target primed by horizontal prime), no enhancement was observed either at sub-threshold or at above-threshold regions (Fig. 4a; maximal enhancement 0.04 ± 0.012, n=3 observers). Facilitation was location-specific as well: when the prime GS ($\omega = 4$ cpd, $\sigma = 0.15°$) was shifted 0.45° of visual angle upwards from the target position, no facilitation was seen across various prime GS contrasts (Fig. 4b; maximal enhancement 0.03 ± 0.017, n=3 observers). 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 different primed eye - target eye combinations: left-left 0.17 ± 0.017, right-right 0.16 ± 0.017, right-left 0.02 ± 0.012 and left-right 0.02 ± 0.012 log units, mean±SE, n=3 observers).

An important property of perceptual memory is its fragility to more recent visual stimulation [5, 12, 21], while further processed memories may survive recent stimuli [21]. We examined whether the memory trace found here is interfered by intervened stimuli during the delay. Another high contrast GS (mask GS: 60% of contrast; otherwise the same orientation, spatial frequency, and size as target GS) was inserted between prime and target. The inter-stimulus interval was 810 ms between prime and mask, and 810 ms between mask and target (Fig. 1 lower panel). The memory facilitation was abolished with the mask GS (Fig. 4c; maximal enhancement 0.02 ± 0.007 log units, n=2 observers), whereas facilitation was observed without mask GS (at SOA=1800 ms), indicating that memory trace can be destroyed by a high contrast Gabor mask.

*Suprathreshold prime contrasts produce facilitatory traces of smaller magnitudes, possibly due to their inhibitory effects [16] and masking properties (Fig. 4c). 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 [20] in IT cortex.

SUMMARY

The main result uncovered by using the Gabor priming paradigm was detection facilitation after presenting a near-threshold GS. The facilitation was long-lasting (16 seconds), far more than perceptual integration time [14]. The memory trace could be erased with a high-contrast mask GS, and is contrast dependent, pointing to a close interface with perception. As the trace is well localized to within target size, but still phase insensitive, it may be related to a stage of visual processing with limited spatial integration, such as the second stage of spatial filtering [16]. Results from visual texture discrimination [22] and from lateral masking [23] studies point toward long term plasticity at the second stage of filtering. Indeed, our STM memory shares the same characteristics of feature selectivity found in perceptual learning, such as for eye, orientation, and location [22, 23]. Together with the findings of neuronal response selectivity in the monkeys primary visual cortex [24], our results suggest that STM can be retained within the primary visual system. This retention may have a role in the consolidation process of neuronal activity into visual long-term memory [23, 25].

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FIGURE CAPTIONS

Figure 1

Computer generated Gabor Signals (GS) [15] and their time course. (a) A foveal prime GS followed by a target GS presented at the same foveal location. Both Gabor signals were vertically oriented. The wavelength (λ) and the Gaussian envelope size (σ) were equal to 0.15° for both prime and target, unless otherwise stated. (b) A target GS preceded by both a prime and a mask GS. On each trial, two of these sequences were presented with only one of them containing the target. The observers task was to indicate the sequence (first or second) containing the target.

Figure 2

Contrast detection threshold (relative to no-prime condition, in logarithmic units) as a function of prime contrast (relative to prime threshold, in logarithmic 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 (four observers). (b) Data from experiments where trials of the same and opposite polarity were mixed. Target detection threshold depends on prime contrast, being lowest when prime contrast is about 65% above prime threshold. The effect is independent of the phase relationship between prime and target. In (b) primes were of positive polarity while targets of either positive or negative polarity were presented in random order, GS assumed lower spatial frequencies ($\omega = 0.5\ cpd,\ \sigma = 2°$), both manipulations aimed at minimizing phase effects due to small deviations of eye fixations.

Figure 3

Time course of contrast detection threshold, which is shown as a function of SOA for two observers (YT, IE). Facilitation is observed around 250 msec of SOA, both for control and prime GS (threshold contrast).

Figure 4

Contrast detection threshold of a vertical target as a function of prime GS contrast with SOA 900 ms, (a) for a horizontal prime - three observers, (b) for the displaced prime - three observers. (c) Detection threshold is shown as a function of prime GS contrast with SOA 1800 ms, with a mask GS inserted at SOA = 900 ms (see Fig. 1b) for two observers. Enhancement is not observed in all three cases.

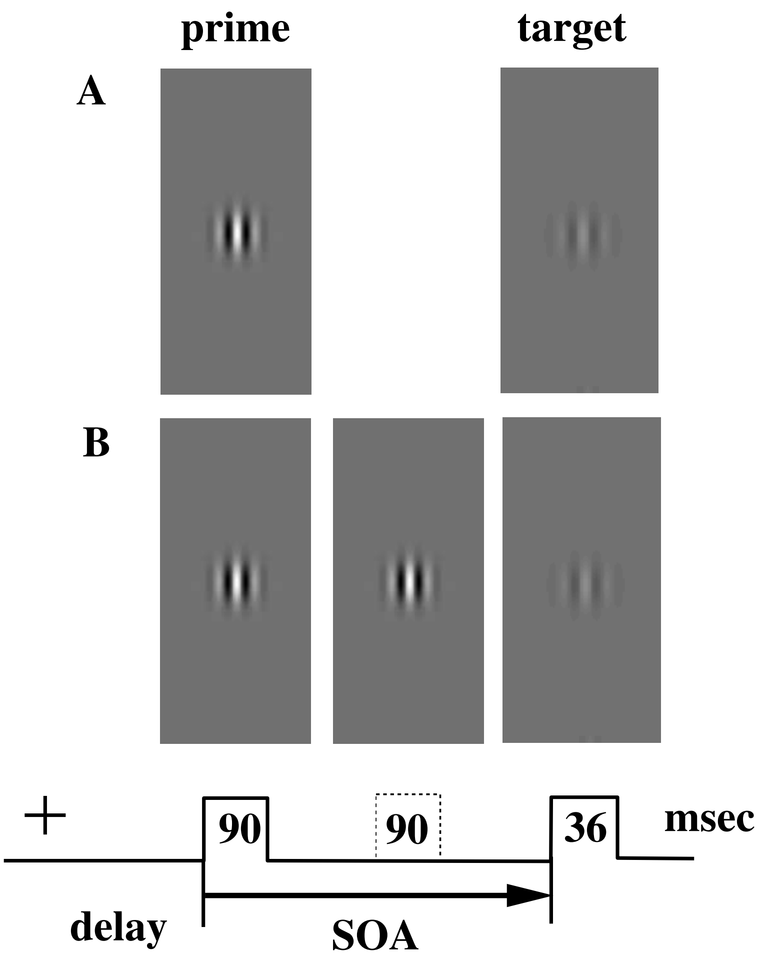

Figure 1:
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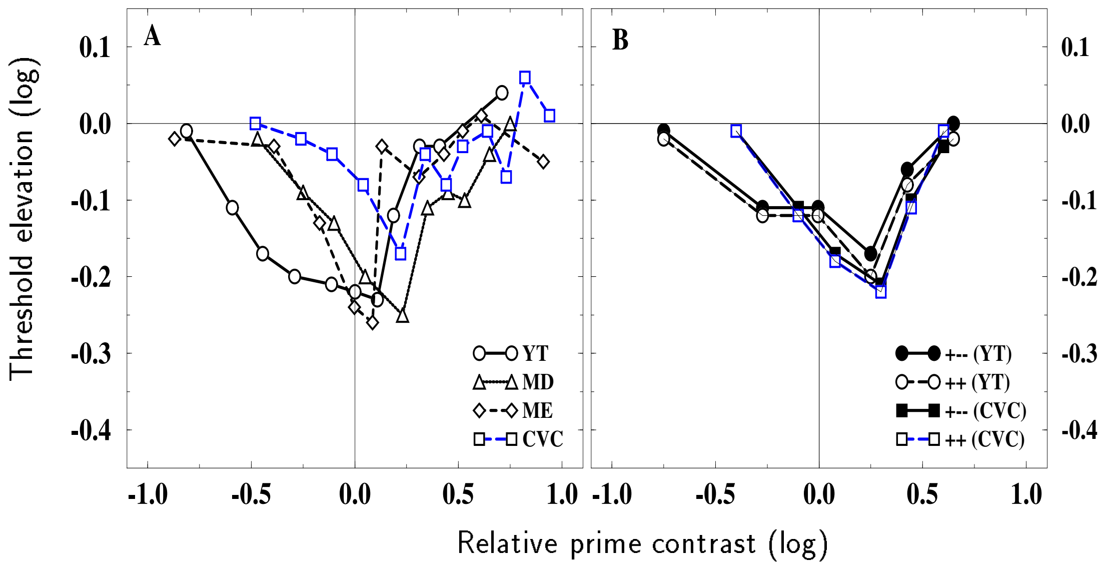

Figure 2:
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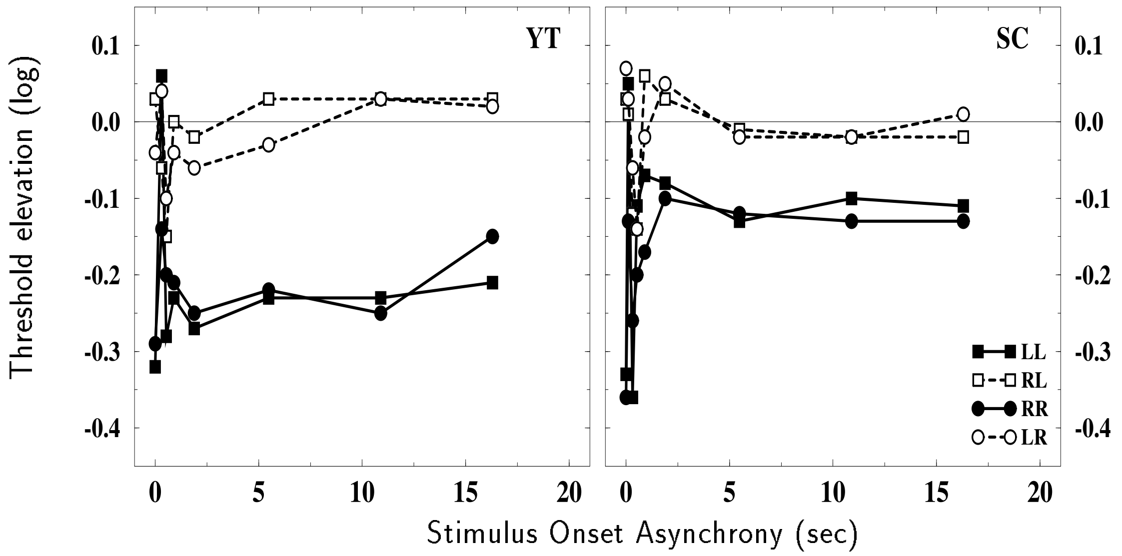

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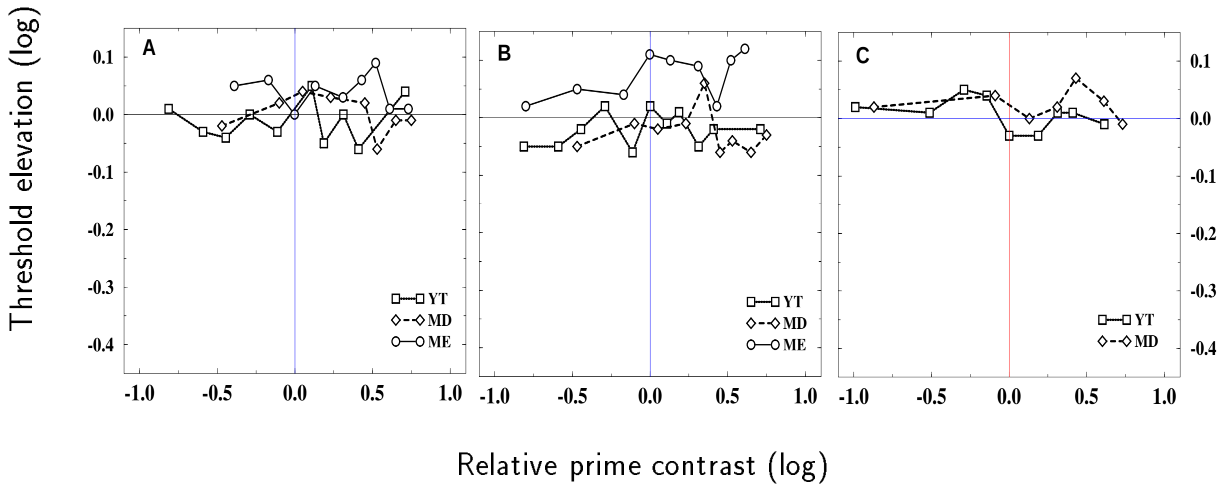

Figure 4:
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