Dynamics of visual short-term memory

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Low-contrast visual stimuli were shown to produce a memory trace, enhancing following target detection for as much as 16 seconds. 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 (dynamic resource allocation). Memory trace 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.

Recently, we reported a perceptual memory for low-contrast visual signals in human vision [1, 2]. In our paradigm, contrast-modulated, spatially-localized sinusoidal gratings (Gabor signals, GSs) preceded similar target GSs with a temporal delay (*Gabor priming paradigm*; see [3] for review of perceptual priming). The main finding was long-lasting detection facilitation of GS targets by low-contrast (at threshold) GS primes, persisting for 16 seconds, far beyond visual integration time [4, 5] or iconic memory range [6, 7]. This facilitation was highly specific to visual features (i.e. location, orientation, spatial frequency, and eye [1]), yet phase insensitive [2] (see also [1]), suggesting the effect occurring at early filtering stages in low-level vision [8]. The facilitation was masked with intervening high-contrast GS stimulation, demonstrating that visual memory is very sensitive to luminance contrast [2]. These findings suggest that low-contrast perceptual signals can generate a long-lasting memory trace within early visual system, probably within the primary visual cortex. Although there is a good body of studies addressing temporal interaction between filters using visual masking [4, 5], sub-threshold summation [9], contrast adaptation [10], or visual persistence [7, 11], it is still unclear which mechanism is responsible for generating long-lasting memory traces [1, 12]. Here we show that temporal-cueing or visual-warning signals [13, 14] are critical to produce short-term visual memory. Furthermore, we show that contrast-dependent facilitation and suppression can occur depending on prime orientation, indicating orientation tuning involved in the generation of visual memory.

RESULTS

In our priming paradigm, a stimulus sequence consisted of a prime GS, followed by a target GS after a temporal delay (Stimulus Onset Asynchrony: SOA, defined as the time between prime and target onsets) [1, 2]. Contrast detection thresholds were measured for a target GS (see Methods). Two experimental conditions were tested: the priming condition, in which prime GSs in addition to peripheral crosses were presented prior to the target, and the control condition, in which prime GSs 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 prime GSs. Different time delays (SOAs) and different prime orientations were tested in separate blocks (Methods). Detection thresholds were plotted as a function of SOA, from SOA=0 (prime and target were overlapped in time thus prime served as a *pedestal*) to SOA=1,800 ms, for the control and two different prime orientations of 0° (identical) and 45° (tilted). Prime contrast was set at the threshold level for each observer.

Thresholds dramatically reduced with temporal-cueing signals for *all* conditions (identical and tilted orientations, and control) at SOA of 360–540 ms, relative to thresholds at SOA=0 **(Fig. 2a, b)**. The optimal facilitation (threshold reduction) was observed with SOA around 500 ms. The magnitude of maximal reduction was 0.22 ± 0.02 (mean±SE, n=4 observers) in logarithmic units for the control, 0.17 ± 0.02 log units for primes identical to target, and 0.11 ± 0.01 log units for tilted primes. This effect occurred due to general temporal-cueing effects (alertness) [13], since threshold reduction was observed in both prime and control conditions. Larger SOAs (> 630 ms) yielded baseline (SOA=0) performance in the control condition. The presence of low-contrast prime with identical orientation yielded threshold reduction of 0.21 ± 0.02 log units (n=4 observers) relative to control at the same SOA. The threshold reduction persisted until 1,800 ms of SOA. Surprisingly, when prime orientation was tilted by 45°, thresholds *increased* at longer SOAs (> 700 ms) by 0.15 ± 0.04 log units (n=4 observers) relative to control, persisting up to 1,800 ms of SOA. Eye dependence was tested by employing monoptic/dichoptic experiments with primes presented either to the same or different eyes to the target (Methods). Facilitation was observed for both monoptic and dichoptic conditions during the first 240–480 ms, either with or without prime GSs, indicating that temporal-cueing effects are *binocular*. Only the monoptic prime condition yielded long-lasting (10.8 seconds) threshold reduction with a magnitude of 0.21 ± 0.03 log units (n=6, observer BC;

Fig. 2c). When prime orientation was tilted by 45°, only the monoptic prime condition yielded suppression (0.15 ± 0.05 log units, n=6, observer YT) with longer SOAs (> 700 ms), while identical orientation preserved facilitation (0.19 ± 0.05 log units, n=6; **Fig. 2d**) in this range, demonstrating *monocular* inhibitory/facilitatory memory traces, consistent with our previous studies [1, 2] (as for monocular-binocular relationship, see Discussion). To assess contrast dependency together with orientation dependence of the long-lasting effect, different prime contrasts were tested with different orientations. SOA was fixed at 900 ms, about 6 times larger than the one where classical temporal summation was observed [4, 9], thus well within a range of visual short-term memory [1, 2, 3, 11]. Detection threshold **decreased** (facilitation) with prime contrast around threshold, when prime and target orientations were identical (both 0°) **(Fig. 3)**, in accordance with our previous study [2]. Threshold **increased** (suppression) at around threshold prime contrast when prime GS was tilted by 15°– 60°. Suppression disappeared (0.01 ± 0.04 log units, n=2 observers, at threshold) when prime orientation was orthogonal (tilted by 90°). Both facilitation and suppression depended on prime contrast, occurring only when prime contrast was low: maximal suppression (0.21 ± 0.04 log units, 2 observers) and maximal facilitation (0.31 ± 0.03 log units, 2 observers) were observed just around prime contrast threshold **(Fig. 3)**. When prime contrast was 3 to 4 times above threshold, both suppression and facilitation disappeared. These results indicate that memory facilitation and suppression depend on orientation *and* contrast.

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 prime GSs, so that temporal-cueing effects can be tested independently of prime GS effects. First, peripheral crosses were presented for duration of 90 ms as a pure temporal cue, then a prime GS was presented for 90 ms after a delay (CPA, Cue–Prime Asynchrony; **Fig. 4**). A target GS was presented after another interval (PTA; Prime–Target Asynchrony). The interval between temporal-cueing signals and target GS was fixed at 900 ms, and different intervals between temporal-cueing signals and prime GS (CPA) were tested (**Fig. 4**, CPA=900–PTA). Baseline threshold was measured without prime GS, 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 Figure 5. Different prime orientations ($0°$, $15°$, and $45°$) were tested in separate sessions. Threshold reduction was observed with PTA at 0 ms (0.20 ± 0.03 log units, n=3 observers), depending on orientation, gradually disappeared with PTA around 300 ms, possibly reflecting a sensory integration process [4, 9]. Threshold enhancement appeared again (0.39 ± 0.04 log units, 3 observers) with PTA at 500–600 ms for all prime orientations. This enhancement effect remained with PTA at 700–900 ms for identical primes (0.22 ± 0.04 log units, 3 observers), while threshold suppression was observed (0.15 ± 0.02 log units, 3 observers) for tilted ($15°$ or $45°$) 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 prime presentations, suggesting an optimal gating process of prime memory generation within this time window. Based on the data presented in **Fig. 5**, 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 establishment.

If specific timing signals, such as temporal cueing or automatic alerting [13], 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, temporal uncertainty was introduced between prime–target intervals; each block of trials consisted of three intervals (SOAs; 0, 500, and 900 ms), one of which was randomly selected on each trial. Thus, observers cannot adapt to a specific timing. Both control and prime conditions were tested with temporal uncertainty (mixed SOA condition) in different sessions. In the prime condition, two orientations ($0°$ and $45°$) were tested. As a comparison, both orientations were tested with SOAs fixed in blocks (fixed SOA condition). Results show that facilitation with the fixed SOA at 500 ms for both orientations disappeared with temporal uncertainty **(Fig. 6)**. Furthermore, both facilitation (with $0°$ prime) and suppression (with $45°$ prime) at SOA 900 ms also disappeared with uncertainty. The threshold reduction at SOA=0 (discrimination) was less affected; facilitation for both orientations remained with temporal uncertainty. These results indicate that temporal uncertainty inactivates temporal-cueing effects, or attention processes, inducing destruction of inhibitory/facilitatory memory traces, while perceptual facilitation (pedestal effect) remains unaffected.

DISCUSSION

We found that temporal-cueing signals 300–500 ms prior to targets produced a general detection threshold reduction, either with or without prime GSs. This general facilitation was associated with prime facilitation and suppression in longer SOAs, since both general threshold reduction at SOA 500 ms, and prime facilitation (with $0°$) or suppression (with $45°$) at SOA 900 ms disappeared when timing information was not provided (temporal uncertainty). This suggests a close association between attentional modulation and memory establishment processes. Contrast sensitivity was enhanced with identical prime orientation ($0°$), but suppressed with tilted prime orientations ($15°$–$60°$), indicating orientation tuning processes of visual memory. Facilitation and suppression were observed when prime contrast was low, where the peak sensitivity was narrowly tuned near prime threshold, probably reflecting inhibitory processes operating above threshold [2, 15, 16, 17, 18]. Both facilitation and suppression were eye-specific, showing that traces are generated at a monocular level of processing. Together with results of feature specificity in the visual system (orientation, position, eye [1, 2], and spatial frequency [1]), our results suggest that visual memory is generated at early stages of visual processing.

The general facilitation at around SOA 300–500 ms transfered between eyes, pointing towards a binocular process. This is in line with visual-alertness or arousal studies in attention psychophysics [13] and neurophysiology [14], suggesting that top-down binocular signals and stimulus-driven monocular signals interact at early levels of visual processing. One possibility for such a mechanism would be a global top-down process that *gates* local bottom-up signals [19, 20] in the primary visual cortex, where monocular cells converge on binocular cells [21, 22]. This gating process may involve timing-related processing in cortico-cortical networks [23] or cortical-subcortical networks [24]. Memory traces may also be generated by dynamic changes in visual receptive fields [25], with low contrast primes triggering an increased receptive field selectivity for basic visual features such as orientation (possibly involving receptive field expansion [26]), thus enhancing primed orientation sensitivity while reducing sensitivity to other orientations within the initial orientation bandwidth (45°) [22, 25, 27] without affecting the orthogonal orientation. High contrast stimulation would, on this account, reset receptive fields parameters.

Methods

Display: Stimuli were presented as gray 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 $9.6^o \times 9.6^o$ area. The mean display luminance was 38 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 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 $9.56^o \times 6.72^o$ area. In the dichoptic/monoptic experiments, stimuli were viewed with CrystalEyes E-1 stereo glasses with optic shutters that alternate in 120Hz synchronized with the monitor. An 8-bit RGB mode was used, and Gamma correction was applied to produce linear behavior of the displayed luminance. The mean display luminance was 40 cd/m^2. The viewing distance was 100 cm.

Stimuli: 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**, Stimulus Onset Asynchrony: SOA, defined as the time between prime and target onsets). Gabor signals (GSs) were generated by calculating equation the $GS(x,y) = \cos(\omega x)\exp(-\frac{x^2+y^2}{\sigma^2})$, $\omega = 6.7$ *cpd*, $\sigma = 0.15°$. Stimulus intensity distribution was defined by $I(x,y) = I_0 + A_{GS}GS(x,y)$, 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. Each prime and target interval included two high-contrast crosses to minimize temporal uncertainty (size: $0.46° \times 0.46°$ each, 90 cd/m^2, located randomly in the area between 1.7° and 0.85° from the target, aligned at a direction of $\theta = -45°$ but of $\theta = 45°$ in prime displays). Different orientations, SOAs, and contrast of prime GS were tested.

Contrast thresholds for targets were measured using a temporal two-alternative forced choice (2AFC) procedure. Each trial consisted of two *stimuli sequences*, only one of which had a target. Before each trial, a 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 to activate the trial sequence: a uniform luminance interval (450 to 900 ms, randomized, 1 ms bin), a first prime-interval (90 ms), a uniform luminance interval (=SOA–90 ms), a first target-interval (90 ms), a uniform luminance interval (1710 to 2160 ms, randomized), a second prime-interval (90 ms), a uniform luminance interval (=SOA–90 ms), 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, prime GSs were not presented ($A_p = 0$) and only peripheral crosses were presented in the prime interval. All displays were viewed binocularly. In the monoptic and dichoptic experiments, the non-stimulated 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. Inter-trial-interval (ITI, an interval between the second target and the fixation in the next trial) was at least 3 seconds or more, depending on observer's reaction time.

Procedure: The observers were asked to determine which of the two target-intervals contained the target GS (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 8 amplitude reversals (a *block* of trials) with the log-amplitude values at the last 6 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 $A_p = 0$).

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FIGURE CAPTIONS

Figure 1

Sample *stimulus sequences:* Prime and target displays contained two peripheral crosses (size and distances are not in scale in this figure). **(a)** No prime GS is presented, only crosses serving as temporal cues (=control condition). **(b)** A foveal prime GS, followed by a target GS at the same foveal location. Prime and target orientations are identical (here 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 (detection). Different SOAs were tested in different sessions.

Figure 2

Time course of detection facilitation and suppression. **(a), (b)** Dependence of contrast detection threshold on prime-to-target asynchrony (SOA) for control (no prime), prime orientation 0°, and 45° (observers MD, YT). 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. Prime GS contrasts, A_p: MD - $0.05 I_0$, YT - $0.08 I_0$ for both orientations. **(c)** Thresholds are shown for observer BC as a function of longer SOAs (up to 10.8 sec), for monoptic and dichoptic prime/control conditions. Prime orientation was 0°. Each datum point is the average of six or more measurements with the same eyes (prime-target: left-left, right-right) for the monoptic condition, and different eyes (left-right, right-left) for 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 seconds) facilitation. Prime GS contrast, A_p: $0.10 I_0$. **(d)** Orientation dependency (primes 0° or 45°, observer YT) for monoptic and dichoptic prime/control conditions. Each datum point is the average of six 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° prime) and suppression (with 45° prime) were observed only for the monoptic prime condition with SOA > 700 ms. Prime GS contrast, A_p: $0.10I_0$ for both orientations.

Figure 3

Orientation and contrast dependence of detection. Contrast detection threshold (relative to control, in logarithmic units) as a function of prime contrast (relative to prime threshold, in logarithmic units), with SOA fixed at 900 ms. Five prime orientations ($0°, 15°, 45°, 60°,$ *and* $90°$) were tested in different sessions, while target orientation was kept at 0°. Maximal enhancement and suppression were obtained when prime contrast was close to its threshold, independent of individual sensitivity. Target (prime) GS thresholds, $A_t = A_p$: $0.08I_0$ ($0.16I_0$) for 0°, $0.09I_0$ ($0.17I_0$) for 15°, $0.08I_0$ ($0.15I_0$) for 45°, $0.07I_0$ ($0.14I_0$) for 60°, and $0.08I_0$ ($0.16I_0$) for 90°, for observer MD (YT).

Figure 4

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

Figure 5

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. Suppression was observed around PTA 900 ms. These imply separated processes of *perceptual integration*, *attention*, and *memory*, respectively (see text). Target GS thresholds at SOA 900 ms, A_t: MD - $0.08I_0$, CVC - $0.08I_0$, YT - $0.16I_0$. Prime GS contrasts, A_p: MD - $0.05I_0$, CVC - $0.05I_0$, YT - $0.10I_0$ for each orientation.

Figure 6

Effects of temporal uncertainty. Threshold is shown as a function of SOA for control (no prime GSs) and two prime conditions (0° and 45°). Data were averaged across three observers (RO, GM, YT). 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 orientations as well as memory facilitation/suppression at SOA 900 ms, while perceptual facilitation (SOA=0) for both orientations remained. Prime GS contrasts, A_p: RO - $0.04I_0$, GM - $0.04I_0$, YT - $0.07I_0$ for each orientation.

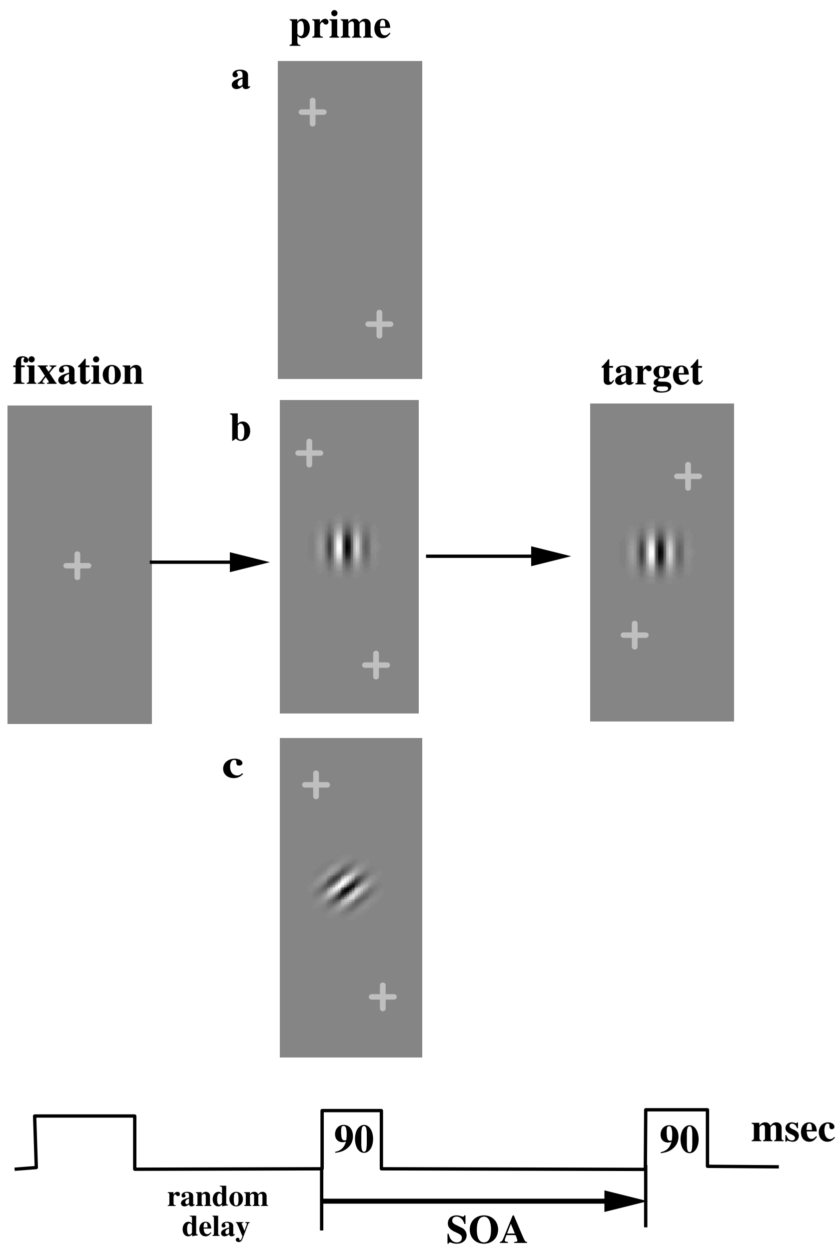

Figure 1:
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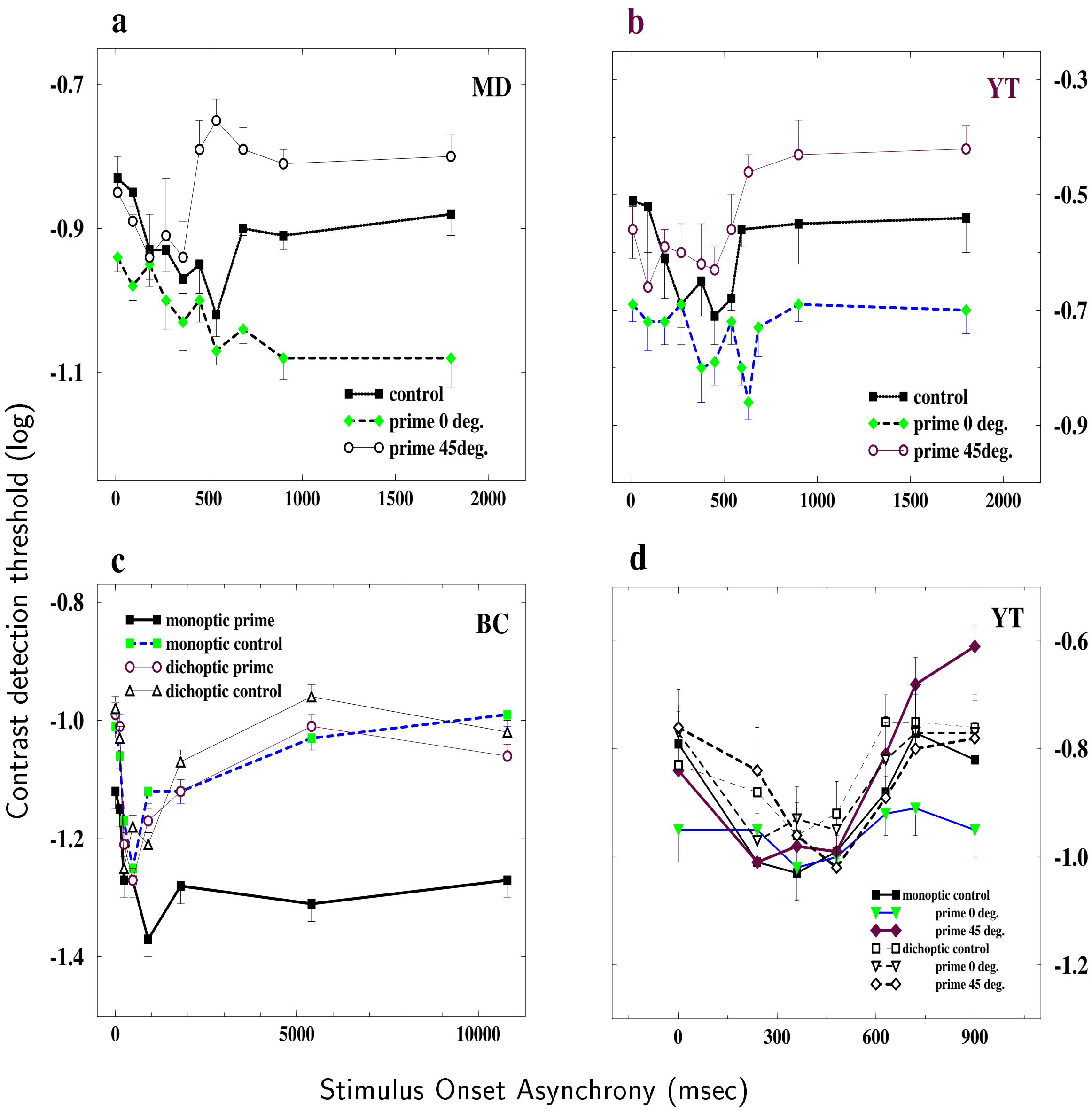

Figure 2:
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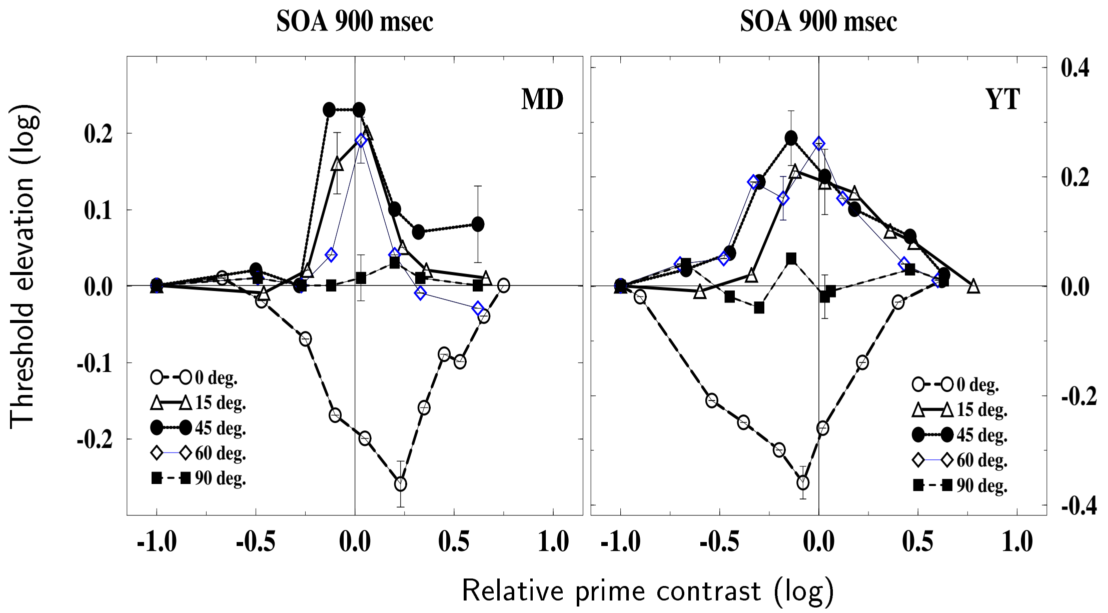

Figure 3:
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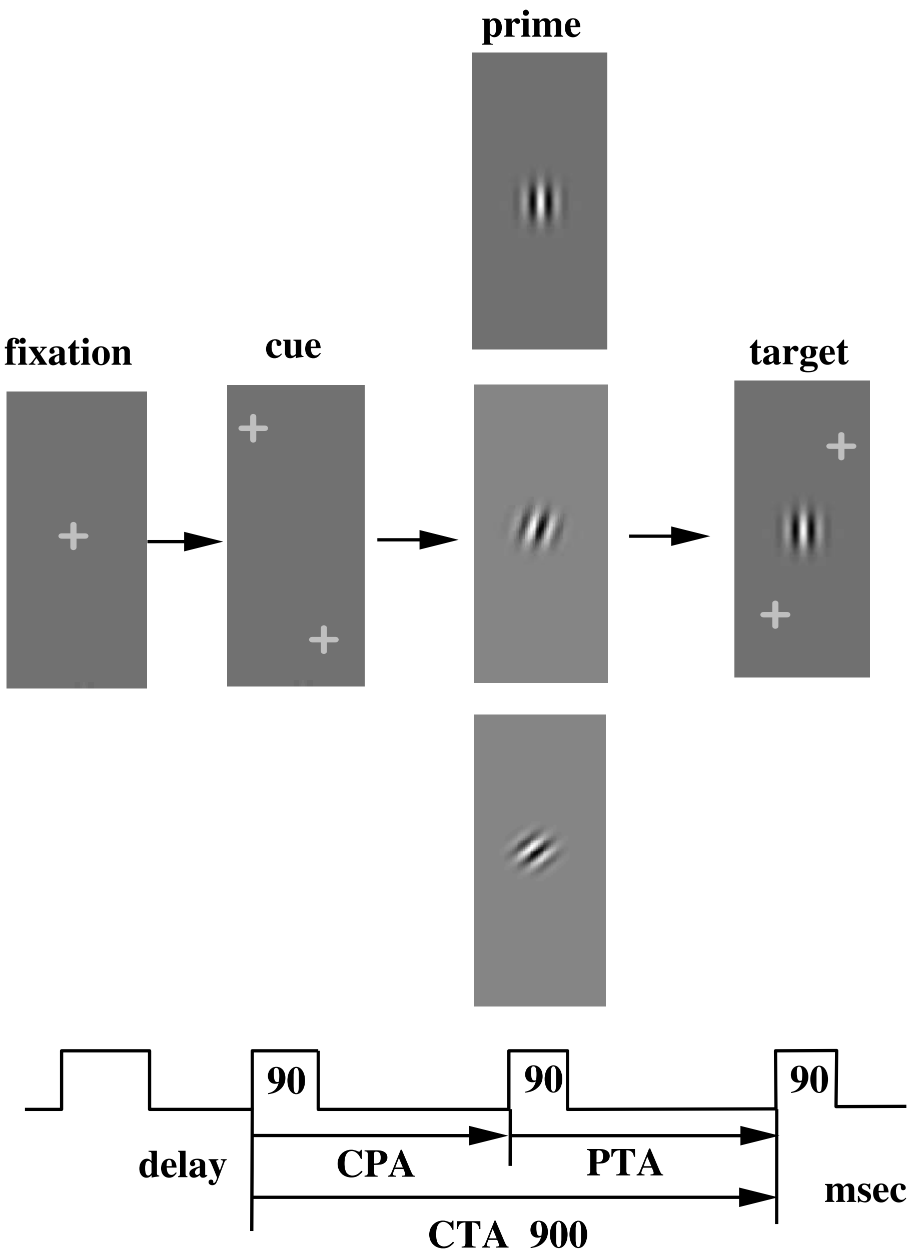

Figure 4:
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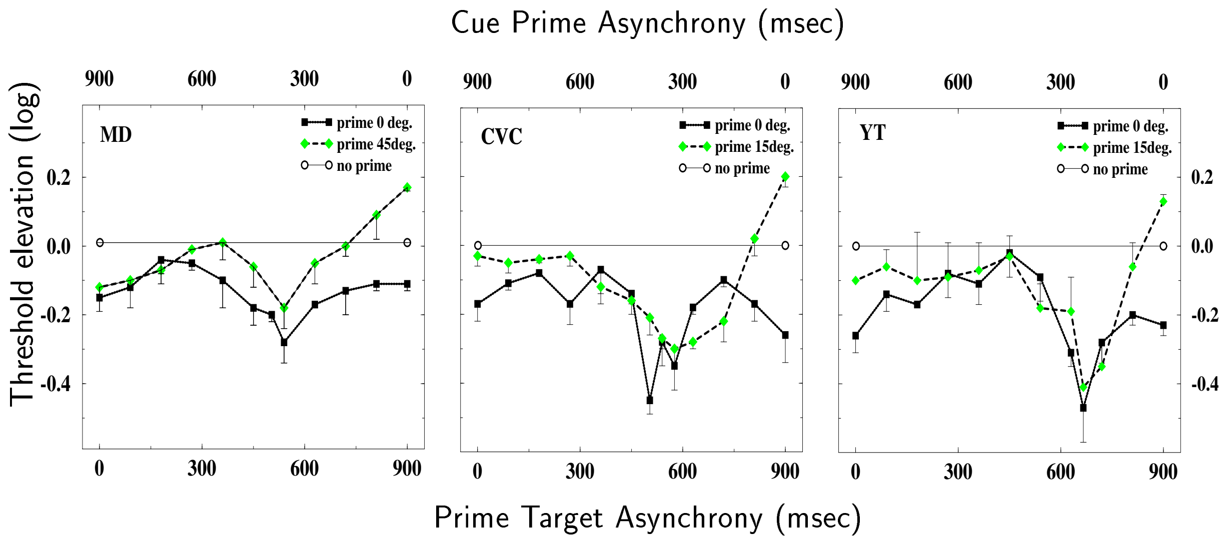

Figure 5:
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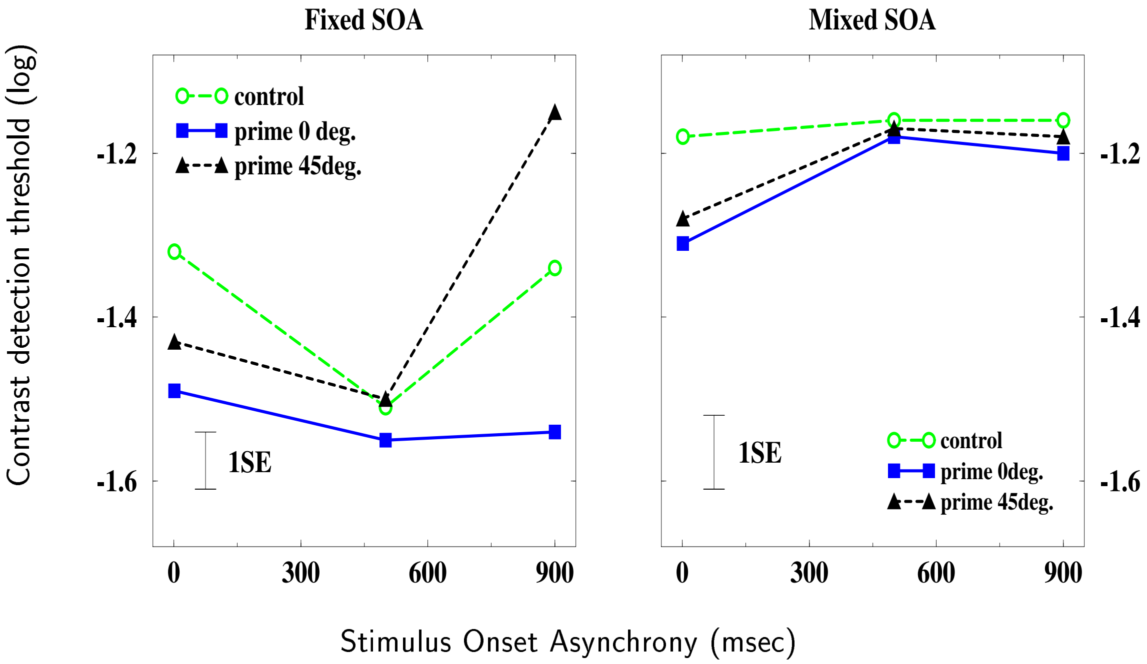

Figure 6:
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