

# Central factors contributing to para-contrast modulation of contour and brightness perception

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## Abstract

Following up on a prior study of contour and brightness processing in visual masking (Breitmeyer et al., 2006), we investigated the effects of a binocular and dichoptic para-contrast masking on the visibility of the contour and brightness of a target presented to the other eye. Combined, the results support the contributions of several cortical processes to para-contrast: (1) two central sources of inhibition, one long-latency and prolonged and the other short-latency and brief; (2) binocular rivalry suppression; and (3) a facilitatory effect peaking at different SOAs for the contour and the brightness tasks, reflecting; (4) known properties of two separate cortical systems, one a fast contour-processing pathway and the other a slower brightness-processing pathway.

**Keywords:** Contour, Brightness, Cortical processing, Suppression, Facilitation

## Introduction

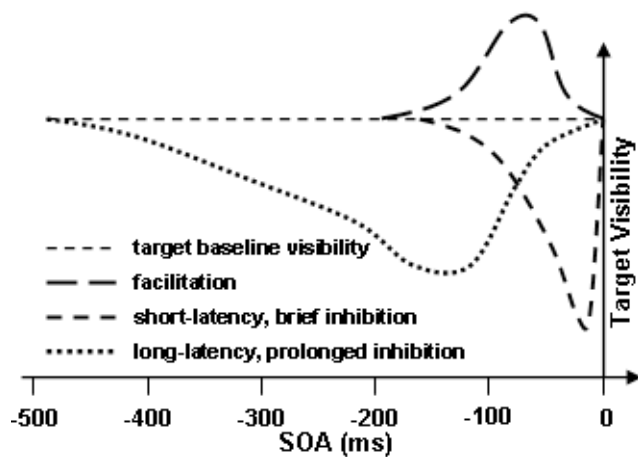
Para-contrast is a form of visual masking in which the visibility of one briefly flashed stimulus, called the target, can be affected by a briefly flashed second stimulus, called the mask, which precedes the target by varying stimulus onset asynchronies (SOAs). In a prior study (Breitmeyer et al., 2006), we showed that para-contrast (as well as meta-contrast) masking can reveal systematic differences between fast contour processing and slower surface brightness-processing systems. Moreover, from the results of that study, we suggested that para-contrast revealed two *cortical* sources of inhibition, one short-latency and brief, and the other long-latency and prolonged, as well as a central facilitatory effect. The short-latency, brief inhibition was attributed to the surround inhibition found in visual receptive fields (Benardete & Kaplan, 1997; Maffei et al., 1970; Poggio et al., 1969; Singer & Creutzfeldt, 1970), while the prolonged, long-latency inhibition was attributed to cortical sources of prolonged, long-latency inhibition known to occur in cats (Berman et al., 1991; Connors et al., 1988; Nelson, 1991) and assumed to occur also in humans (see Fig. 1). However, since binocular viewing of stimuli was used throughout that study, resulting in activation of monocular as well as binocular channels, it is not entirely clear that the obtained inhibitory effects of para-contrast on target visibility have a binocular origin; subcortical as well as cortical monocular activity may also have contributed substantially (or entirely) to the effects.

Moreover, we attributed the facilitatory effect of a para-contrast mask (see Fig. 1) on the visibility of a following target to “perceptual retouch.” A transient stimulus activates not only stimulus-specific sites in the visual cortex but also the nonspecific subcortical (midbrain/thalamic) arousal system. This system in turn, via ascending projection fibers, facilitates activity at the stimulus-specific cortical sites. The enhanced stimulus-specific activity in the visual cortex produced by the ascending projections from the nonspecific subcortical arousal system in turn results in an enhancement of stimulus visibility. The latter enhancement is known as perceptual retouch (Bachmann, 1988, 1994).

While such facilitatory effects at cortical levels may indeed exist, it is possible that the stimulus-specific activities generated separately by the mask and the following target also could interact at cortical and subcortical monocular levels, e.g., through temporal response summation within visual neurons responding to the two stimuli, to affect facilitation of the target’s visibility. In order to establish more firmly the role of these three putative cortical modulatory effects we compare in the current study the effects of para-contrast mask on the following target when both stimuli are viewed binocularly to effects obtained dichoptically, when the target and mask are presented to separate eyes.

Performance in visual masking studies depends not only on differences between these two viewing conditions (Schiller & Smith, 1968) but also on the criterion content used by an observer (Hofer et al., 1989; Kahneman, 1968; Stoper & Mansfield, 1978; Ventura, 1980). Criterion content is determined by the task requirements and refers to the stimulus dimension along which an observer is asked to make his or her perceptual judgment about the target. As in our prior study (Breitmeyer et al., 2006), in the

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**Fig. 1.** Schematic diagram of the three modulatory influences: (1) facilitation, (2) long-latency, prolonged inhibition, and (3) short-latency, brief inhibition, on a target's visibility produced by a preceding paracontrast mask.

present study, we required observers to make target visibility judgments based on the contour and on the surface brightness of the target. According to recent theoretical modeling (Grossberg, 1997; Grossberg & Howe, 2003), supported by neurophysiological findings (DeYoe & Van Essen, 1988; Lamme et al., 1999; Xiao et al., 2003; Xiao et al., 1999), a cortical boundary-contour-system (BCS) and a cortical feature-contour-system (FCS), corresponding to the parvocellular, P-interblob and P-blob streams in the cortical object object-processing pathway (Grossberg, 1994), process a visual object's contour and surface properties, respectively. Our present study, by using a dichoptic viewing condition, assures that effects of the para-contrast mask on the targets contour and brightness visibility reflect properties of these central BCS and FCS systems.

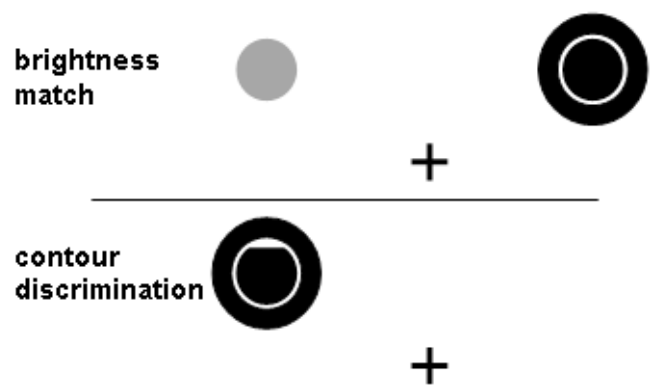
## Materials and methods

### Observers

Four observers, including the authors BB (58-year old male) and RZ (26-year old male), were used in all experiments. The other two volunteer observers, a 22-year and a 28-year old female, were practiced psychophysical observers but naïve as to the purposes of the experiment. All observers gave informed consent and had normal or corrected-to-normal vision. All experimental procedures were conducted in accordance with principles embodied in the Helsinki Code.

### Stimuli and Apparatus

The experiment was performed in a dark room. The stimuli were displayed at 100 Hz frame rate on a Sony Trinitron color monitor. A visual stimulus generator (VSG2/5) card manufactured by Cambridge Research Systems controlled stimulus presentation and response recording. Fig. 2 illustrates the stimulus configuration used in the brightness judgment and in the contour discrimination tasks. The fixation mark consisted of a small ( $0.4^\circ \times 0.4^\circ$ ) dark ( $0.5 \text{ cd/m}^2$ ) cross in the center of the screen. In the brightness judgment task, the stimuli consisted of a ring mask, which spatially



**Fig. 2.** Examples of target disks and mask rings used in the brightness match procedure (upper panel) and in the contour discrimination procedure (lower panel). Plus signs designate the fixation cross. See text for further details.

surrounded the right disk of a two-disk display. The right disk served as the target and the left disk as the comparison stimulus. The target and comparison disks had a diameter of  $0.85^\circ$  and the mask ring had inner and outer diameters of  $0.85^\circ$  and  $1.27^\circ$ , respectively. The right target-mask configuration and the left comparison disk were centered  $1.4^\circ$  above fixation and  $1.6^\circ$  to the right and left of fixation, respectively. The luminance of the target disk and the mask ring was  $30.5 \text{ cd/m}^2$ . Against a uniform background luminance of  $95 \text{ cd/m}^2$ , this corresponded to contrasts of 52%. The observer could adjust the luminance of the comparison disk adaptively. The mask and the target were presented for 10 ms each. In the contour identification task, the same mask ring was used. However, the target could consist of a complete disk, a disk with a  $0.37^\circ$  wide upper contour deletion (shown in Fig. 2), or a disk with the lower contour deletion of the same size. The target (preceded by the surrounding mask) could be shown at the upper left or upper right stimulus locations described above. For both tasks, the following target-mask SOAs were used: 0,  $-10$ ,  $-20$ ,  $-40$ ,  $-60$ ,  $-80$ ,  $-110$ ,  $-140$ ,  $-170$ ,  $-200$ ,  $-350$ ,  $-500$ , and  $-750$  ms (negative SOA values designating that the mask preceded the target). Moreover, a no-mask (target only) condition was also used in order to obtain baseline performance for both the brightness match and the contour identification tasks. In binocular viewing, all stimuli were centered on the video screen. Using a haploscopic mirror arrangement for dichoptic viewing, the target and the fixation cross were presented to the left eye, and the mask and fixation cross were presented to the right eye.

### Procedure

An experimental session consisted of four blocks of trials, one devoted to the brightness-matching task under binocular viewing, another to the brightness-matching task under dichoptic viewing, a third to the contour discrimination task under binocular viewing, and a fourth to the contour discrimination task under dichoptic viewing. Within each block, the order of para-contrast SOAs, ranging from  $-750$  to 0 ms and including the baseline, no-mask condition, was randomly varied. Regarding the brightness-matching task, at each SOA the luminance of the match stimulus changed according to the subject's response. Initially the comparison disk was either clearly brighter or darker than the target disk. On any

trial, the observer's task was to report, by pressing one of two response buttons, which of the two disks, the target or the comparison, appeared brighter. The point of subjective equality (PSE) was estimated by a 1-up 1-down staircase procedure. If the comparison disk appeared darker than the target disk on a trial, its luminance was increased stepwise on the next trial. Conversely, if the comparison disk appeared brighter than the target disk, its luminance was decreased on the next trial by the same amount. For the initial three reversals, the step size was an increase or decrease of 2.4 cd/m<sup>2</sup>. After the third reversal, the step size was an increase or decrease of 0.24 cd/m<sup>2</sup>. At this step size luminance reversals of the comparison disk were recorded, and the PSE of the target disk for a given SOA was calculated as the average of the last six-luminance reversals of the comparison disk. Each observer served in four experimental sessions. Order of task within a session was counterbalanced across sessions. As a result, four average brightness-match values were obtained for each observer at each SOA, from which the observer's overall mean was calculated. These served as the data for off-line statistical analysis. For the contour identification task, the procedure was the same except for the following changes. At each SOA, the location of the target-mask sequence was randomized across 30 trials, with half of the trials devoted to the upper left location, the remaining half to the upper right location. Of the 30 trials, 10 were devoted to each of the three possible target contours. Order of target contours was randomized across the 30 trials. After each trial, the observers were required to indicate, by pressing one of three keys, which of the three targets was presented. If the observers did not see the target, they were asked to guess. Here an observer's proportion of correct contour identifications was based on 120 trials at each SOA. These proportions again served as data for off-line statistical analysis.

*Experiment 1: Comparison of binocular and dichoptic para-contrast effects on target contour and brightness perception*

In the present experiment, we explore the effects of a para-contrast mask on the target's contour and brightness visibility when the target and mask are viewed binocularly, compared to similar effects when the target and mask are viewed dichoptically. Each of the four observers ran in the following four experimental conditions: (1) binocular viewing/contour task; (2) binocular viewing/brightness task; (3) dichoptic viewing/contour task; and (4) dichoptic viewing/brightness task. Each observer served in four daily sessions, and in a daily session, each observer was run in all four conditions. The order of presentation of the four experimental conditions was counterbalanced across the four observers; and for each observer across the four days.

*Results and Discussion*

The results are based on the log of normalized target visibilities. In the brightness match task, target brightness visibilities at each SOA were normalized relative to the target's brightness match obtained in the baseline, no-mask condition. In the contour identification task, target contour visibilities were normalized relative to the range of correct-response proportions obtained, at the upper limit, in the baseline, no-mask condition, and at the lower limit (when the target was invisible), by a guessing probability of 0.33. Both brightness match and contour identification tasks tended to yield para-contrast functions with a number of nonmonotonocities. In particular, the functions show not only suppression of visibility over intermediate ranges of SOA values but also some counteract-

ing facilitation of visibility over shorter ranges. These trends can be unraveled by taking a closer look at the results of the three-way (Task × Viewing × SOA) ANOVA. Of the three main effects, only that of SOA was significant ( $F_{12,36} = 9.24, p < .001$ ). This main effect is evident from inspection of Fig. 3, which shows that there is an overall decrease of target visibility (averaged across all experimental conditions) as the SOA changes from -750 to 0 ms. Note, however, that the overall function also shows clear non-monotonocities. Although target visibility is not affected by the mask at SOAs below -350 ms, (1) it decreases from -350 ms to a local minimum at -110 ms, then (2) increases to a local maximum at -40 ms, before (3) decreasing again to a local minimum at -10 ms. These effects of the para-contrast mask replicate those reported by Breitmeyer et al. (2006). The first one reflects the existence of a long-latency, prolonged inhibitory process, the second, a facilitatory process, and the third a short-latency, inhibitory process.

Of the two-way interactions, those between Viewing and SOA ( $F_{12,36} = 5.54, p < .0005$ ) and between Task and SOA ( $F_{12,36} = 2.79, p < .01$ ) were significant. The three-way interaction between Task, Viewing and SOA also was significant ( $F_{12,36} = 10.65, p < .001$ ). Fig. 4a show the results separately for the four viewing by task conditions over SOAs ranging from -750 to 0 ms; and Fig. 4b shows the results on an expanded time scale over SOAs ranging from -200 to 0 ms. The three-way interaction is reflected in two different ways in which the Task × SOA interaction mentioned above expresses itself as a function of viewing condition. First, as shown in Fig. 4b, with binocular viewing (solid symbols) the contour and brightness visibility functions intersect twice, at -80 and at -10 ms; however, with dichoptic viewing the functions intersect only once at an SOA of -80 ms. Second, with binocular viewing the contour visibility function shows a local minimum at an SOA of -10 ms, revealing the existence of the short-latency, brief inhibitory process; whereas with dichoptic viewing that minimum shifts to an SOA of 0 ms.

This shift could be due to several factors. For one, with dichoptic viewing and despite a binocularly fused fixation point, fixation disparities could result from normal vergence dynamics (Patel et al., 2001; Schor et al., 1986). Consequently, the disk-target presented to one eye and the ring-mask presented to the other may not be concentric (i.e., may be shifted) with respect to retinotopic coordinates. This may in turn result in the greatest suppression of target visibility at an SOA of 0 ms. On the other

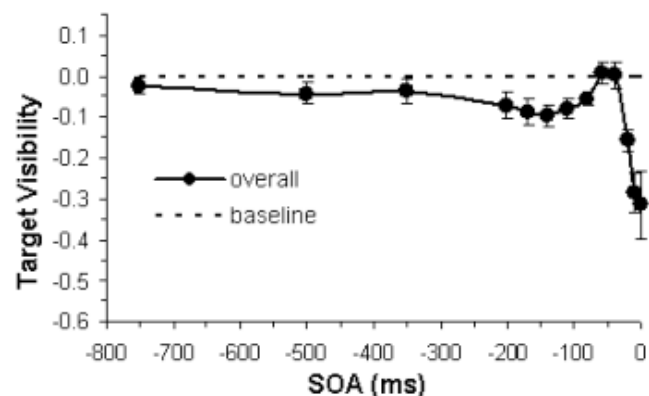
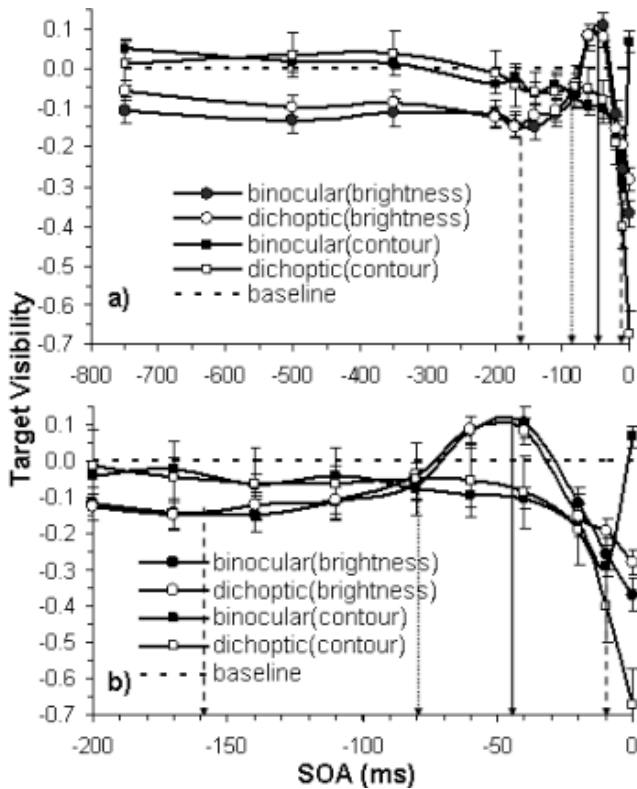


Fig. 3. Overall target visibilities as a function of target-mask SOA. Error bars indicate  $\pm 1$  SEM.



**Fig. 4.** Target contrast and contour visibilities as a function of target-mask SOA shown separately for all four combinations of task (brightness match, contour discrimination) and viewing (binocular, dichoptic) (a) for SOAs ranging from  $-750$  to  $0$  ms and (b) for SOAs ranging from  $-200$  to  $0$  ms. Dashed vertical lines indicate local minima of visibility produced by inhibitory processes; dotted and solid vertical lines indicate local maxima of visibility produced by facilitatory processes. Error bars indicate  $\pm 1$  SEM.

hand, with dichoptic viewing one also introduces the possibility that binocular rivalry suppression contributes to the total masking effect (Schiller & Smith, 1968). Although these two proposed processes are not mutually exclusive, the following experiment was designed to address which of them offers a better explanation of the shift.

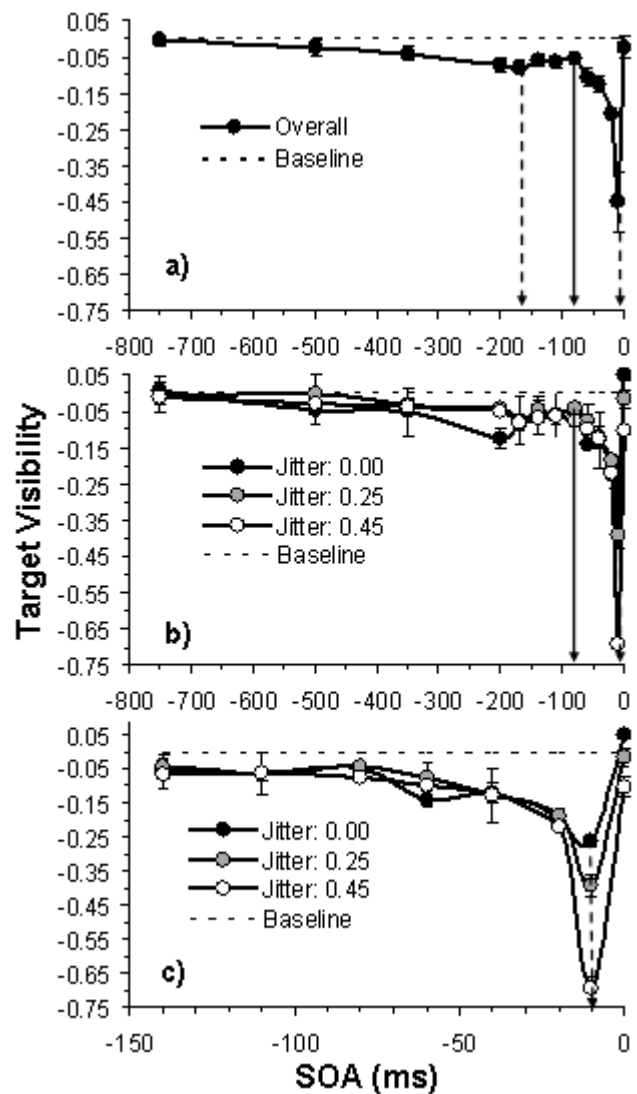
*Experiment 2: The Possible Roles of Fixation Disparity and Binocular Rivalry Suppression in Dichoptic Masking*

If the misalignment of the monocular retinotopic coordinates of the target and mask stimuli produced by fixation disparity during dichoptic viewing was the cause of the shift of optimal para-contrast suppression from  $-10$  ms to  $0$  ms, then artificially introducing such misalignments under binocular viewing also should produce such a shift. To induce such retinotopic misalignment of the target and mask we systematically varied the degree of horizontal displacement of the center of the ring-mask relative to that of the disk-target. In this experiment, we used only the contour-discrimination task since relative to the brightness-matching task it tended to yield a somewhat stronger suppression of visibility at an SOA of  $-10$  ms. Across trials the relative misalignment was equally often to the left and to the right and could take on the following values;  $0$  (perfect alignment),  $0.25$ , or  $0.45$  deg, corre-

sponding to  $0$ ,  $29.4$ , and  $52.9\%$  of the target-disk diameter. Four observers serving in Experiment 1 also served in the present experiment. Separate blocks of trials were used for each level of misalignment. All viewing was binocular. Other than these specific conditions, the procedure was identical to that used in Experiment 1.

*Results and Discussion*

The results are again based on the log of normalized target visibilities. A Misalignment X SOA repeated measures ANOVA revealed a nearly significant main effect of Misalignment ( $F_{2,2} = 16.33, p = .058$ ), a significant main effect of SOA ( $F_{12,12} = 33.44, p < .0001$ ) and significant effect of the Misalignment X SOA interaction ( $F_{24,24} = 7.73, p < .001$ ). The main effect of SOA is evident from inspection of Fig. 5a, which, like Fig. 3a, shows



**Fig. 5.** Target contour visibility as a function of target-mask SOA for (a) overall, and (b) and (c) for varying levels of target-mask misalignments, in deg visual angle, as indicated. Dashed vertical lines indicate local minima of visibility produced by inhibitory processes; solid vertical lines indicate local maxima of visibility produced by facilitatory processes. Error bars indicate  $\pm 1$  SEM.



that overall there is a decrease of target visibility (averaged across all three misalignment conditions) as the SOA changes from  $-750$  to  $0$  ms. Note again that the overall function again indicates clear nonmonotonicities. Target visibility decreases from  $-750$  ms to a local minimum at  $-170$  ms (indicated by dashed-line arrow), then 2) increases to a local maximum at  $-80$  ms (indicated by solid-line arrow), before 3) decreasing again to a local minimum at  $-10$  ms (indicated by dashed-line arrow). These effects of the para-contrast mask again replicate the inhibitory and facilitatory effects reported by Breitmeyer et al. (2006). The significant Misalignment X SOA interaction is illustrated in Figs. 5b and 5c, which show the target visibility as a function of SOA for SOAs ranging from  $-750$  to  $0$  ms and (on an expanded time scale) from  $-170$  to  $0$  ms, respectively. While target visibility is approximately equal across the three levels of misalignment for SOAs ranging from  $-170$  to  $0$  ms, note that the target visibility at the optimal para-contrast SOA of  $-10$  ms decreases from a value of  $-0.26$  to  $-0.60$  as the target-mask misalignment increases from  $0$  to  $0.45$  deg. This shows that the retinotopic misalignment of the target relative to the surrounding mask *does not produce a shift* of the optimal para-contrast masking SOA from  $-10$  to  $0$  ms, but rather it *enhances the optimal suppression at the SOA of  $-10$  ms*. Thus, of the two proposed processes, binocular rivalry suppression and dichoptic fixation disparity, the former provides the better explanation for the shift of the optimal para-contrast SOA from  $-10$  to  $0$  ms under dichoptic viewing of target and mask stimuli.

### General Discussion

The results overall indicate similarities as well as differences between a target's contour and brightness visibilities during para-contrast masking, and they are discussed in terms of the three processes depicted in Fig. 1. Two of these processes are inhibitory. One, a suppressive effect, is produced by the center-surround antagonism within receptive fields of the form-processing P pathway as proposed by Breitmeyer et al. (2006). It is known that the inhibitory surround activation of visual receptive fields is slower by 10 to 20 ms than activation of the center region (Benardete & Kaplan, 1997; Maffei et al., 1970; Poggio et al., 1969; Singer & Creutzfeldt, 1970). One would then expect that the surrounding mask has to precede the target by SOAs of  $-10$  to  $-20$  ms to obtain optimal suppression of target-induced excitatory activity. These intrachannel, center-surround inhibitory effects are most likely fast and of a short duration (Connors et al., 1988). Such processes would explain our current findings of an optimal suppression of the target's brightness and contour visibilities at an SOA of  $-10$  ms, at least when the target and mask are viewed binocularly.

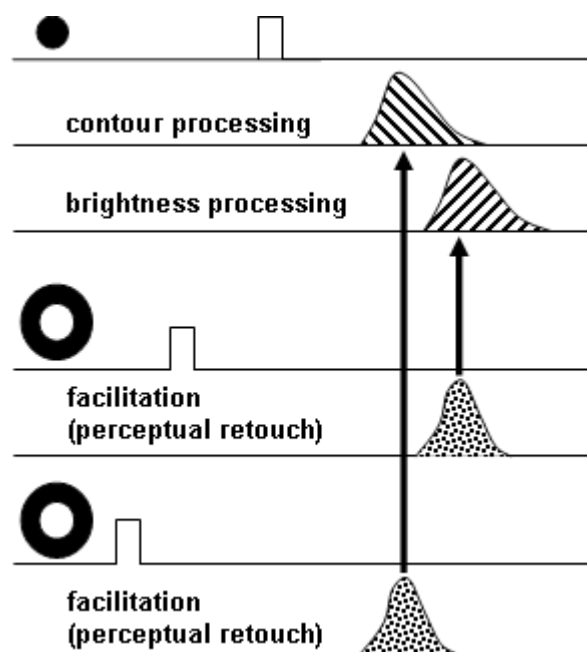
However, with dichoptic presentation, additional suppression due to binocular rivalry can also contribute to masking, as originally suggested by Schiller and Smith's (1968) masking study. The combined results of Experiments 1 and 2 indicate that rivalry suppression may be particularly strong when the two target and mask stimuli are presented simultaneously (Meese & Hess, 2005), thus leading to a shift of optimal suppression from an SOA of  $-10$  ms to an SOA of  $0$  ms.

Besides the short-latency short-duration inhibition and the effects of binocular rivalry suppression, our para-contrast results indicate that an additional longer-latency inhibitory effect lasts for up to 400 ms or more. As indicated in the empirical results shown in Figs. 3a and 5a, suppression of target visibility can begin when the mask precedes the target by about 400 ms (or more). Evidence

for the long-latency and prolonged inhibition has been found in visual cortex of cat (Berman et al., 1991; Connors et al., 1988; Nelson, 1991). Our results therefore are consistent with the existence of a similar inhibition also in the human visual cortex.

In addition, our para-contrast results show that a prior mask can have not only suppressive effects on target visibility but also a counteracting facilitating effect. According to perceptual retouch theory (Bachmann, 1988, 1994), a stimulus activates not only afferent pathways that project via the lateral geniculate nucleus to specific visual cortical areas but also pathways projecting to nonspecific activating systems in the subcortical brain-stem and midbrain, which in turn project to the specific cortical areas and enhance activity there (Singer, 1979; Steriade & McCarley, 1990). The response of the subcortical nonspecific system is generally slower by about 50–60 ms than that of the cortical specific systems. Hence, if a stimulus is delayed by about 50 ms relative to a prior one, the faster specific cortical activity generated by the following stimulus will be maximally enhanced by the slower nonspecific subcortical activation produced by the preceding stimulus. As a result, the visibility of the second of two stimuli will be maximally enhanced. The strength of perceptual retouch, i.e., of facilitation, should depend on the strength of the preceding mask relative to the target. Increasing mask contrasts ought to increase the facilitatory effect, a result reported by Breitmeyer et al. (2006). In the present study, the target and mask stimuli had a contrast of 0.52; and therefore the facilitation effect of the mask may not have been optimal. Our concern, however, was not to optimize either the facilitation or the suppressive effects of the mask, but rather to demonstrate that these effects occur at central cortical levels.

Fig. 6 illustrates how a facilitation produced by the slower nonspecific subcortical arousal system could enhance the visibility of a target's brightness and contour during para-contrast. For instance, the facilitatory effect on visibility of a target's brightness is maximal when the mask precedes the target at an SOA of a few



**Fig. 6.** Schematic diagram showing how a (long-latency) facilitatory process (solid arrows) produced by the mask optimally affects target contrast and contour visibilities at short and long target-mask SOAs.

tens of milliseconds. In addition, it is evident from Fig. 6 that the facilitatory effect on visibility of a target's faster contour processing is maximal when the mask precedes the target by a slightly larger SOA. This is supported by the current findings. As shown in Figs. 4a and 4b, maximal enhancement for the target's brightness visibility occurs at SOA = -40 ms. On the other hand, as shown in Figs. 4b and 5a, for the target's contour visibility, the maximal enhancement appears to occur at and SOA of -80 ms. This difference of 40 ms between the optimal enhancement SOAs for brightness and contour visibility can be explained by the fact that contour processing occurs about 40 ms faster at cortical levels than does surface brightness (Lamme et al., 1999). It should also be noted that whereas the brightness matching task yields clear facilitation above baseline visibility at SOAs of -60 and -40 ms (see Figs. 3c and 4), the results of the contour discrimination task indicate a weak local facilitation below baseline at SOAs of -110 and -80 ms (see Figs. 3c, 4b, and 5a). This difference may be due to a difference between the psychophysical procedures used to measure target brightness and target contour or due to a stronger short-range inhibitory effect of the mask on the target's contour visibility than on its contrast visibility.

In conclusion, the three neural processes, (1) short-latency and short-duration inhibition, (2) longer-latency and longer-duration inhibition, and (3) facilitation proposed by Breitmeyer et al. (2006) to explain the complex effects of the para-contrast mask on the visibility of brightness and contour visibility of the target most likely act at a central level since they can be obtained with dichoptic as well as binocular presentation of the target and mask stimuli. Of course as previously mentioned, the central facilitation effect of the mask has its origin initially in subcortical activations of the thalamic and midbrain reticular systems; these activations, via ascending projection fibers, in turn facilitate the processing of stimulus features at central cortical sites. Moreover, an additional process of binocular rivalry suppression appears to play a substantial role in dichoptic masking, especially when the target and mask are presented simultaneously. Whether or not these conclusions apply to surface-specifying features other than brightness, such as color or texture, remains to be determined.

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