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The time course of psychophysical end-stopping

Cong Yu *, Dennis M. Levi

College of Optometry, University of Houston, Houston, TX 77204, USA

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Abstract

This study measured the time course of psychophysical end-stopping and compared it with the time course of masking. For a 10′ D6 target on an 18′ D6 pedestal, two abutting end-zone masks (each 13.5′ long) covering the filter end-zones reduce masking. This facilitatory 'end-stopping' effect was measured over a range of exposure durations and stimulus onset asynchronies (SOAs). We found that psychophysical end-stopping has a delayed onset which is around 70–100 ms after stimulus onset, in contrast to masking which is robust immediately after stimulus onset, suggesting intracortical feedback processes in the generation of psychophysical end-stopping. The development course of psychophysical end-stopping is relatively long and lasts for approximately 150–200 ms after stimulus onset, in contrast to that of masking which lasts for approximately 100–150 ms. Our results also showed that end-stopping occurs only when the center mask and the end-zone masks have sufficient temporal overlap, possibly indicating that the feedback process for generating end-stopping is triggered by the activation of the spatial filter center by the center mask. These results are in tune with current knowledge of intracortical feedback modulating activities of receptive fields, and have been incorporated into our model to describe the temporal dynamics within end-stopped spatial filters.

Keywords: End-stopping; Masking; Time course; Intracortical feedback; Spatial filter

1. Introduction

When an elongated stimulus such as a line or a grating is superimposed on a masking object, the contrast threshold for the stimulus is elevated. This masking effect, as recently demonstrated, is influenced by the length of the mask (Yu & Essock, 1996a; Yu & Levi, 1997a). For example, for a small D6 target (the luminance profile of the sixth derivative of a Gaussian) masked by another D6 grating of the same spatial frequency and orientation, the contrast threshold was first elevated, then reduced, with increasing mask length (Yu & Levi, 1997a). The initial elevation of masking may reflect increased pooling of divisive signals which normalize or suppress the response of underlying spatial filters (e.g. Heeger, 1992; Foley, 1994). Masking reaches its peak as the mask fully covers (and thus indicates) the length extent of the spatial filter center (Yu & Levi, 1997a). Further lengthening the mask encroaches on the end-zones of spatial filters and triggers end-stopping, which counterbalances the suppressive normalization and reduces masking (Yu & Levi, 1997a, 1998a).

This psychophysical evidence for cortical receptive field end-stopping (Hubel & Wiesel, 1965, 1968) has been under investigation in a series of studies, and a number of important properties of "psychophysical end-stopping" have been revealed. Psychophysical end-stopping has a cortical origin, as demonstrated by its steep spatial scaling function which resembles the cortical magnification function (Yu & Essock, 1996b), and by its dichoptic transfer (Yu & Levi, 1997b). It is tuned to spatial frequency and orientation (Yu & Levi, 1998a), but is relatively unaffected by the mask polarity (Yu & Levi, 1998b) or phase (Yu & Levi, 1997a), analogous to the phase insensitivity of physiological end-stopping (Tanaka, Ohzawa, Ramoa & Freeman, 1987; DeAngelis, Freeman & Ohzawa, 1994). It is nearly abolished in humans with naturally occurring amblyopia (Yu & Levi, 1997b), which echoes Kennedy and Orban's (1983) report that cats reared in stroboscopic light have a very low ratio of end-stopped neurons. The loss of end-stopping might reflect its general vulnerability to abnormal post-natal visual experience.

* Corresponding author. Fax: +1-713-743-1888; e-mail: yucong@bayou.uh.edu.

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The current study investigates the time course of psychophysical end-stopping in spatial filters and compares it with the time course of masking. Two major factors prompted us to study this issue. Firstly, previous results show that masking is phase sensitive, but psychophysical end-stopping is not (Yu & Levi, 1997a). This phase difference suggests that psychophysical end-stopping may reflect second-order visual information at a later stage of visual processing than conventional masking. Neurophysiologically, receptive field end-stopping is at least partly generated by intracortical feedback in the visual cortex (Hubel & Wiesel, 1965, 1968; Bolz & Gilbert, 1986; Grieve & Sillito, 1991), and can be disabled pharmacologically without disturbing other receptive field properties (Bolz & Gilbert, 1986). Thus receptive field end-stopping is generated at a later stage than other receptive field properties, consistent with our psychophysical results. This distinct property of later processing of end-stopping might be expressed in its time course. Secondly, masking has been partly attributed to a normalization process in which divisive signals pooled from neighboring filters suppress the responses of spatial filters (e.g. Heeger, 1992; Foley, 1994). We have proposed that such a normalization process can be weakened by end-stopping so that the sensitivity of the spatial filter can be at least partially restored. By comparing the time course of masking and end-stopping, we ask how masking and end-stopping interact in the time domain.

We measured the time course of psychophysical end-stopping and masking over a range of temporal conditions, including exposure duration, SOA, and their combinations. Our results show that psychophysical end-stopping has a delayed onset and takes more time to develop than does masking. End-stopping begins to appear around 70–100 ms after stimulus onset, and asymptotes at its full strength at 150–200 ms, in contrast to masking which is robust immediately after stimulus onset and asymptotes around 100–150 ms. Our results also show that end-stopping is strongest when the center mask and the end-zone masks are temporally fully overlapped (0 ms SOA) with sufficient exposure duration. Together these results suggest that psychophysical end-stopping is likely generated by some intracortical feedback processes triggered by the activation of the spatial filter center, consistent with current knowledge of intracortical feedback modulating activities of receptive fields (see Section 4), and in tune with neural mechanisms underlying the generation of physiological receptive field end-stopping. These temporal properties were incorporated into our model to describe the temporal dynamics of interactions between masking and end-stopping which jointly determine the responses of spatial filters.

2. Methods

2.1. Observers

Four observers (two males, DK and YC, two females, LC and QV, aged 19–32) served in this study. All had normal or corrected-to-normal vision. Observers QV and YC were experienced, DK and LC were new to psychophysical experiments and received many hours of training. Only YC was aware of the purpose of the study.

2.2. Apparatus & stimuli

The stimuli were generated by a Vision Works computer graphics system (Vision Research Graphics, Inc.) and presented on a US Pixel P × 19 monochrome monitor. The resolution of the monitor was 1024 × 512 pixels, with the size of each pixel being 0.28 mm horizontal × 0.41 mm vertical. At the viewing distance of 5.64 m, the screen size of the monitor was 3.8° × 3.0°. The frame rate of the monitor was 117 Hz. Luminance of the monitor was made linear by means of a 15-bit look-up table. The mean luminance of the monitor screen was 62 cd/m^2. Experiments were run in a dimly lit room, with a low watt light on the back of the monitor. Viewing was monocular by the dominant eye of each observer (right eye for all observers).

The spatial configuration of the stimulus (Fig. 1) was a spatially localized foveal D6 target centered on another D6 mask of the same spatial frequency (either 1.7 or 8.0 cpd) and orientation (vertical), which was produced by interlacing the target and mask in separate frames. In this way the frame rate for the stimuli (58.5 Hz) was actually half of the monitor frame rate. The spatial frequency bandwidth of the D6 stimuli was 1.0

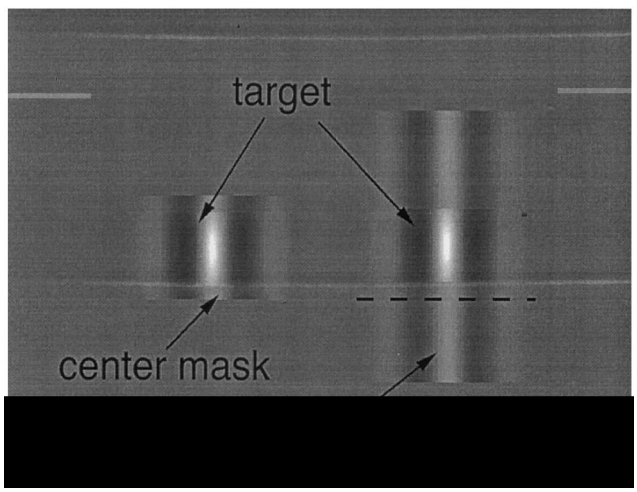

Fig. 1. Stimuli shown in two masking conditions. Left: a D6 target (10′) on a center D6 mask (18′). Right: a D6 target (10′) on a center D6 mask with two additional end-zone masks (45′ overall).

octave. The D6 target was partially blurred by a Gaussian window along its long axis ($\sigma = 4.2'$) and truncated at the target length of 10′. The D6 mask, which was not blurred and always set at a contrast level of 40%, was a central 18′ long D6 grating with or without two abutting 13.5′ long D6 flanks of the same spatial frequency and orientation. Thus the mask was actually either an 18 or a 45′ long D6 grating. Previous experiments (Yu & Levi, 1997a) showed that, for the same 10′ long target, an 18′ long D6 mask produced peak masking and a 45′ long D6 mask (an 18′ D6 grating plus two abutting 13.5′ D6 gratings) produced maximal end-stopping. We thus referred to the 18′ long D6 mask as 'center mask' which we assume masked the center of the putative spatial filters, and the two abutting 13.5′ long D6 gratings as 'end-zone masks' which we assume covered the end-zones. In this configuration, the effect of end-stopping is indicated by the reduction of contrast thresholds from the 'center mask' condition to the 'center + end-zone mask' condition.

To examine the time courses of psychophysical end-stopping and masking, two temporal variables, stimulus onset asynchrony (SOA) and exposure duration, and sometimes their combinations, were manipulated. The target and the mask were either presented together at different exposure durations, or presented at different mask-target SOAs, or the target + center-mask and the end-zone masks were presented at different SOAs at different exposure durations. Details of the temporal properties of stimuli in each experiment will be given later.

2.3. Procedure

Contrast thresholds for the D6 target were measured with a successive two-alternative forced-choice staircase procedure. The mask was presented in each of two stimulus intervals separated by a 400 ms inter-stimulus interval. The duration of the stimulus intervals varied under different SOA and/or stimulus duration conditions and will be specified later. The target was randomly presented in one of the two stimulus intervals. The observers task was to judge which stimulus interval contained the target. Each trial was preceded by a $6.3' \times 6.3'$ fixation cross in the center of the screen which disappeared 100 ms before the beginning of the trial. Audio feedback was given on incorrect responses.

Each staircase consisted of four preliminary reversals and six experimental reversals. The initial contrast of the target was set to be high enough so that the observers would not easily miss the target, and thus was varied across different experimental conditions. The step size of contrast change in preliminary reversals was set at 0.5% and in experimental reversals at 0.125%. Each correct response lowered the target contrast by one step and each incorrect response raised the target contrast by three steps, which resulted in a 75% convergence level of the staircase. The mean of the six experimental reversals was taken as the contrast threshold. An experimental session usually consisted of 9–10 randomly presented conditions, and lasted for about 40 min. Each datum represents the mean of 5–6 replications for each condition, and the error bars represent ± 1 S.E.M.

3. Experiments

3.1. The time course of psychophysical end-stopping

In this experiment, we measured the time course of psychophysical end-stopping by presenting the target and mask together with the same onset and offset at a duration varying from 34–400 ms. Two masking conditions, a center mask (18′) and a center + end-zone mask (45′ overall) masking a 10′ D6 target, as well as two spatial frequencies (1.7 and 8.0 cpd), were used. The rationale of this experiment was simple: if psychophysical end-stopping, like its neurophysiological counterpart, requires intracortical feedback to generate, some amount of processing time would be used by this feedback process, and the end-stopping effect would unfold itself with a latency after stimulus onset. By comparing the center masking and center + end-zone masking as a function of time, we would be able to learn when end-stopping emerges, which would indicate the minimal time required for end-stopping to generate, and when end-stopping reaches its full strength, which would indicate the full time course of the development of end-stopping.

Individual and mean data are presented in Fig. 2a, b, respectively. The mean data (Fig. 2b) have been fitted with an exponential equation $\mathrm{Th} = \mathrm{a}e^{-t/\mathrm{tc}} + b$ (Th, threshold; t, duration; tc, time constant; a and b, constants) to estimate the time constant of each function. Contrast thresholds associated with the center mask (filled circles) and the center + end-zone mask (unfilled triangles) are nearly identical at the shortest durations, at both 1.7 and 8.0 cpd, suggesting zero end-stopping immediately after stimulus onset. However, after a delay of around 70 ms at 1.7 cpd and 100 ms at 8.0 cpd, end-stopping emerges as the center + end-zone masking functions start to depart from the center masking functions and show lower contrast thresholds, consistent with the cortical feedback assumption. This end-stopping effect gains its strength with increasing duration before asymptoting at its maximum around 200 ms at 1.7 cpd and 150–200 ms at 8.0 cpd. Once fully developed, the end-stopping effect reduces thresholds by approximately a factor of 2.5 at 1.7 cpd and a factor of 1.6 at 8.0 cpd on the average as compared to the center masking functions. Fig. 2c

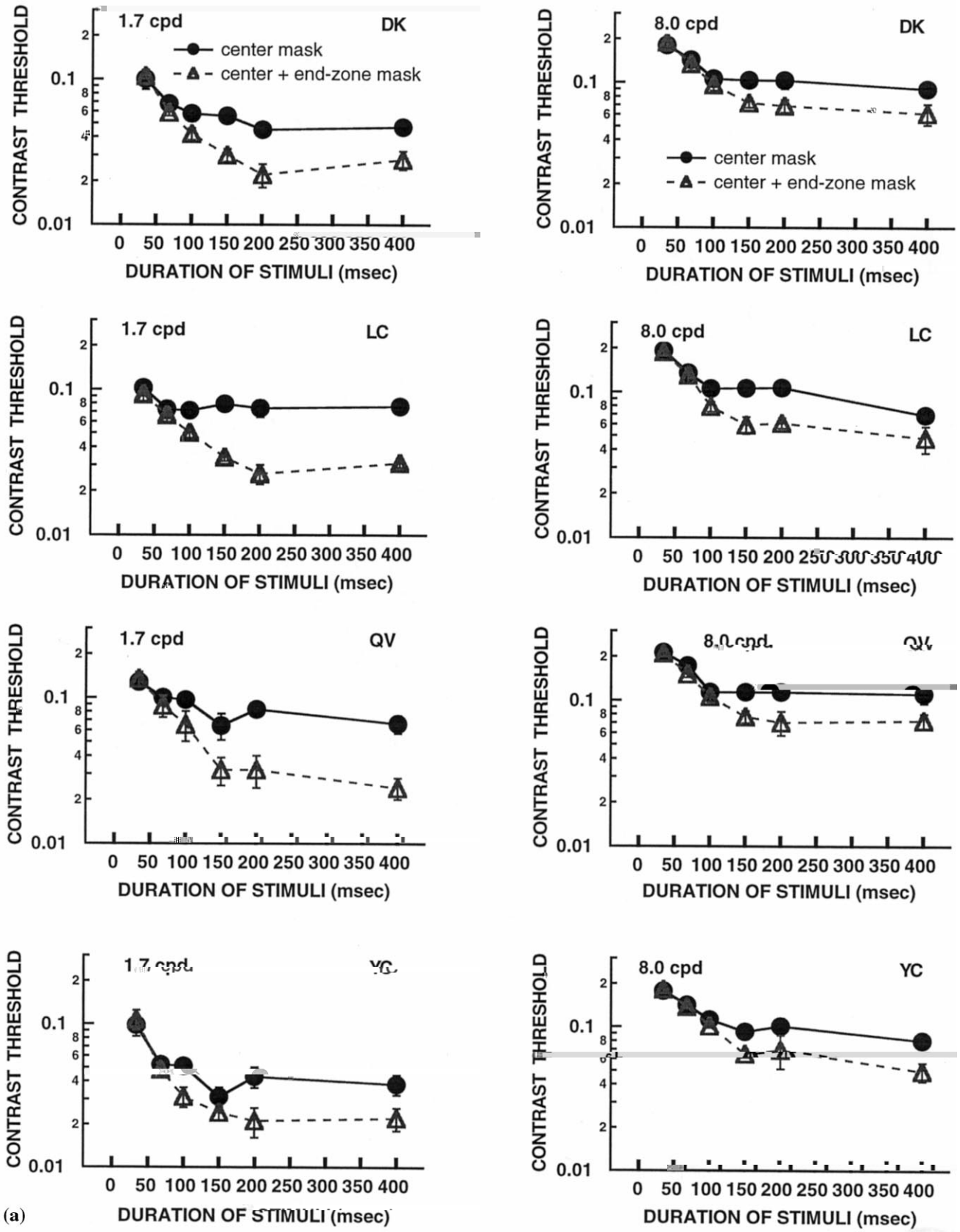

Fig. 2. The development of psychophysical end-stopping as a function of the stimulus duration. The target and mask were presented together with the same onset and offset. (a) Individual results. (b) Mean results and their fitting by an exponential equation $Th = ae^{-t/tc} + b$ to estimate the time constant tc. (c) A direct view of the time course of psychophysical end-stopping: the ratio of sensitivity (1/threshold) of center + end-zone masking and center masking plotted as a function of stimulus duration.

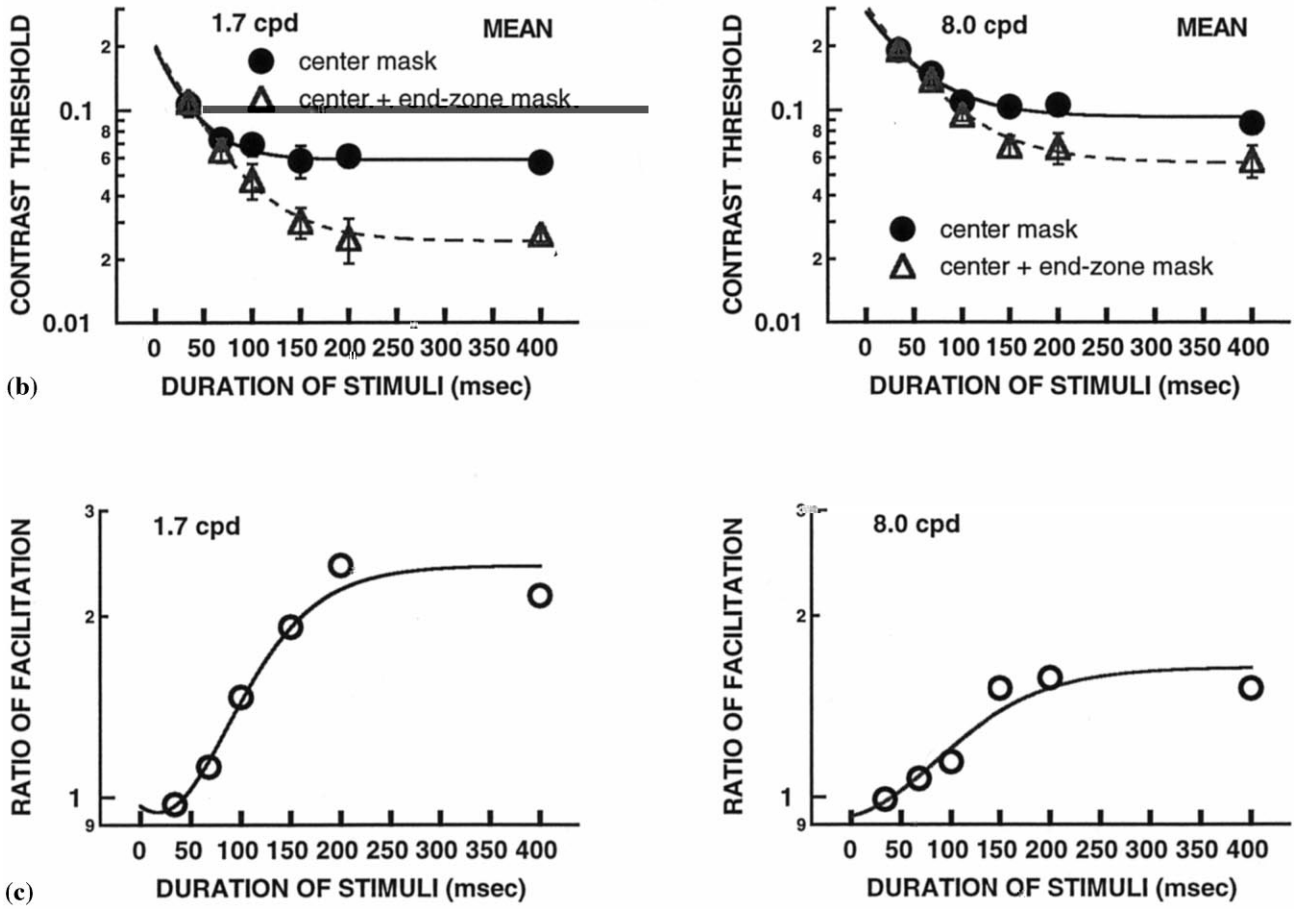

Fig. 2. (*Continued*)

provides a direct view of the time course of psychophysical end-stopping which shows how end-stopping rises and asymptotes across time as indicated by the ratio of sensitivity (1/threshold) in the two masking conditions.

In contrast to the development course of psychophysical end-stopping, the center masking functions asymptote much earlier, about 100–150 ms after stimulus onset at both spatial frequencies. As shown by the data fitting in Fig. 2b, the time constant tc, which indicates the duration at which 63% of the asymptote value is obtained, is 32 ± 6.6 ms for the center masking function, 47 ± 3.1 ms for the center + end-zone masking function at 1.7 cpd, 49 ± 9.7 ms for the center masking function and 56 ± 7.0 ms for the center + end-zone masking function at 8.0 cpd. The nature of the center masking function and the difference of time constants between the center masking function and center + end-zone masking function will be further discussed later.

At very brief exposure durations, the temporal domain of the stimulus is governed by high temporal frequencies. We conducted a control experiment to test whether zero end-stopping at very brief durations actu-

center masking functions: masking and target detection. The asymptote could reflect the time course of either masking, or target detection, or a combination of both. However, previous evidence suggests that for targets at a spatial frequency ≥ 1.5 cpd, which includes 1.7 and 8.0 cpd used in this study, detection performance generally asymptotes at an exposure duration of approximately 1 s (Legge, 1978), and the shape of the function is unaffected by the size of the target (Harris & Georgeson, 1986). The 1 s asymptote for detection is a factor of 7–10 longer than the duration at which center masking functions asymptote. Thus it seems safe to conclude that the asymptote in center masking functions is little affected by target detection and mainly reflects the characteristics of the time course of masking.

To test this notion further, we also measured the temporal dynamics of center masking at 1.7 and 8.0 cpd with a probe-on-flash paradigm (Fig. 4, top panel). The D6 target (10′ long) was presented briefly (50 ms) on a long-lasting (430 ms) D6 mask (18′ long, the center mask). The target had a delayed onset relative to the mask, with the mask-target SOA varying from 8.5 to 380 ms. The individual results (thin lines) and their mean (thick lines) are shown in the bottom two panels of Fig. 4 for each spatial frequency. For the convenience of comparison, the y-axes have the same range of 0.6 log units in each panel. At 1.7 cpd, contrast thresholds are highest at the shortest SOA (8.5 ms) and decrease with longer SOAs, asymptoting at approximately 110 ms on the average, except for a rebound at the longest SOA (380 ms) contributed by two observers. At 8.0 cpd, masking is robust at 8.5 ms SOA with an average of contrast thresholds higher than 20%. (The detection threshold for the same target when not masked is near 10% as measured from one observer (YC)). Masking reaches its maximum at an SOA of about 110 ms with very little decrease thereafter. The overall (center) masking effects are consistent with Bowen, Laine and McKernon (1997) and Wilson and Kim (1998), and the timing difference of maximal masking has been attributed to the activation of transient or sustained pathways by stimuli at low or high spatial frequencies (Bowen et al., 1997). As Wilson and Kim (1998) suggested, these results indicate the time course of masking as a result of divisive gain control in human vision[1]. The asymptote and peak constants obtained from the probe-on-flash experiments closely match the asymptote constants in earlier center masking functions, providing converging evidence on the time course of masking.

Thus, we conclude that masking is robust immediately after stimulus onset, and reaches a constant state at 100–150 ms, in contrast to psychophysical end-stopping which has a delayed onset at approximately 70–100 ms, and completes its development around 150–200 ms.

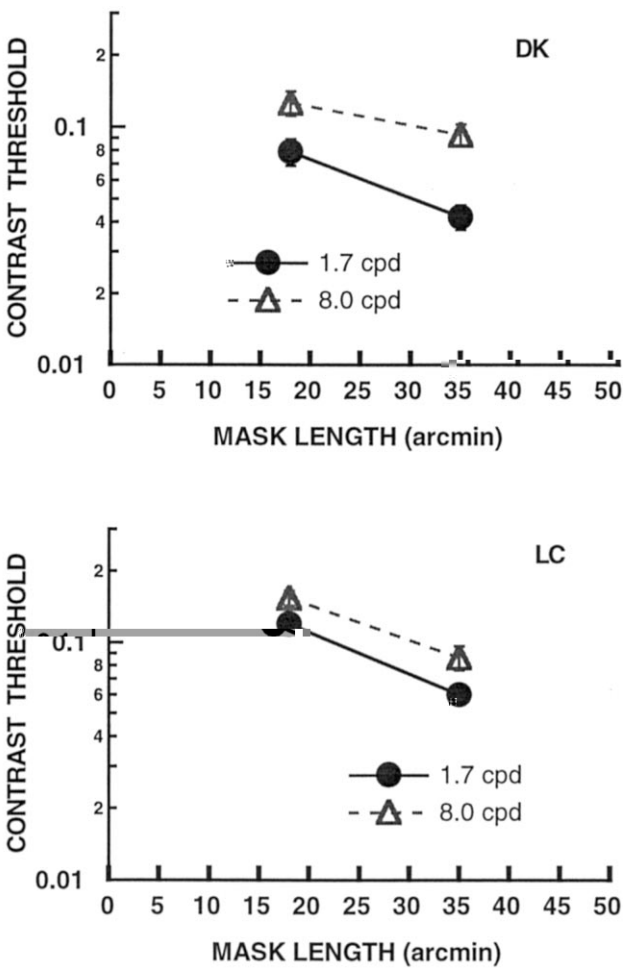

Fig. 3. Psychophysical end-stopping effects for stimuli temporally modulated at 15 Hz for 400 ms.

3.3. Temporal dynamics of interactions between the center mask and the end-zone masks

As suggested earlier, when the target and the mask are presented together, end-stopping requires at least 70–100 ms to develop, suggesting cortical feedback in the generation of psychophysical end-stopping. In this experiment, we studied the temporal dynamics of interactions between the center mask and the end-zone masks. Specifically, we asked how the end-stopping effect is influenced by the onset asynchrony of the end-zone masks from the center mask. We expected that the results would establish the optimal timing between the end-zone masks and the center mask which produces the maximal end-stopping effect, and thus indicate how the generation of psychophysical end-stopping, or its underlying cortical feedback, is tempo-

[1] Wilson and Kim (1998) only measured masking at a low frequency (3.0 cpd) which is similar to our 1.7 cpd data.

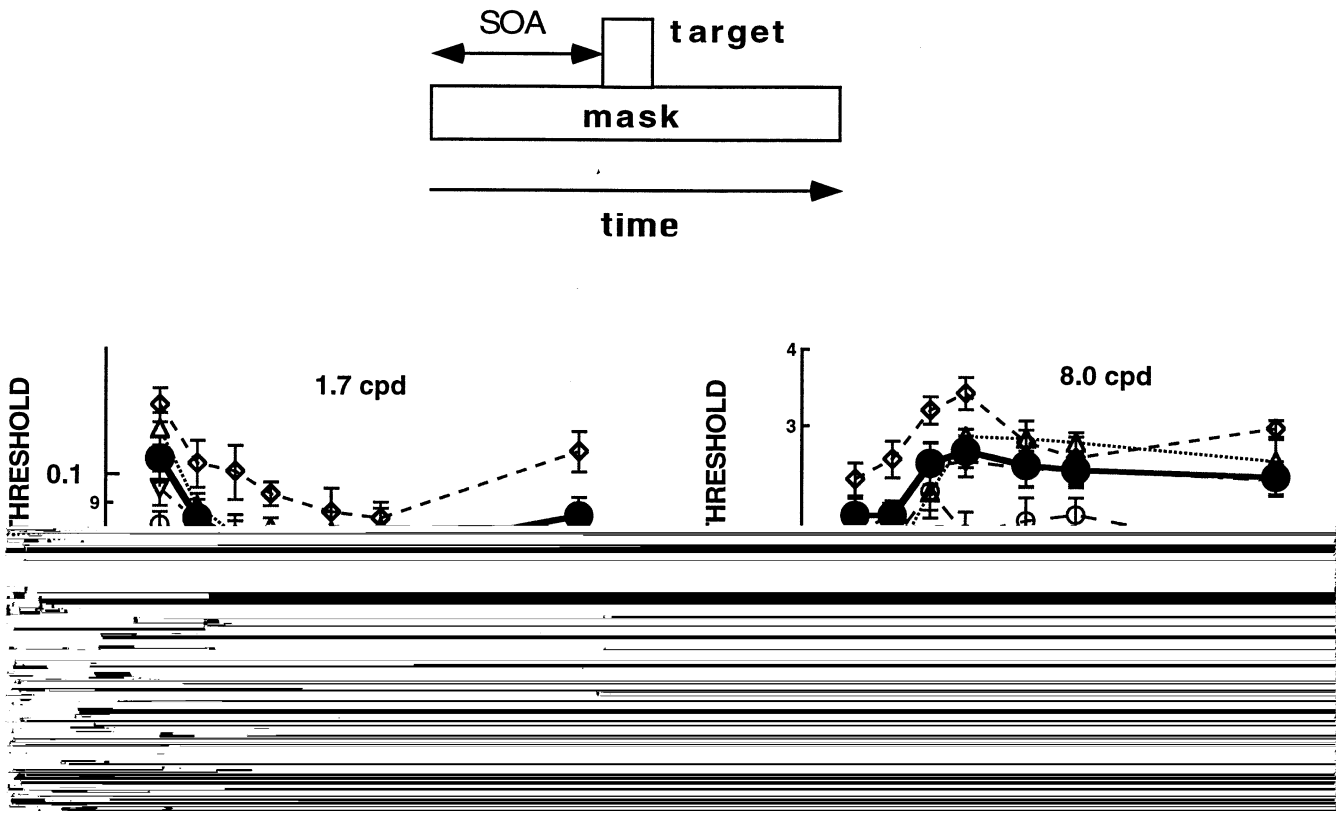

Fig. 4. Temporal dynamics of center masking indicated as the contrast threshold changes as a function of mask-target SOA. The top panel shows the temporal profile of the stimuli. The bottom two panels show results from the same four individuals as in Fig. 2 (thin lines) and their mean (thick lines). The y-axis has the same range of 0.6 log units in each panel.

rally related to the activation of the spatial filter center due to center masking

The spatial content of the stimuli was the same as in earlier experiments (a D6 target masked by a center mask or a center + end-zone mask). However, the target and the center mask were always presented together, while the end-zone masks were presented either earlier (negative SOA) or later (positive SOA) at various SOAs. Each component of the stimuli had the same exposure duration of either 34 or 150 ms, which produced no (34 ms) or substantial (150 ms) end-stopping as in earlier experiments, to examine the interactions between the end-zone mask SOA and the exposure duration. Again two spatial frequencies, 1.7 and 8.0 cpd, were used.

Fig. 5a shows results at 1.7 cpd. The baselines (dashed lines) indicate contrast thresholds measured with no end-zone mask presentation (center mask alone). At a 150 ms exposure duration (Fig. 5a, left column), end-stopping (facilitation) occurs at shorter SOAs, and is strongest when the end-zone masks have the same onset as the target and the center mask (0 ms SOA). When the SOA is longer than about 70 ms, either positive or negative, facilitation changes to suppression. The suppressive effect is slightly stronger at positive SOAs where the end-zone masks have a later onset, probably because the end-zone masks following spatially non-overlapped target at intermediate SOAs produce metacontrast masking (Breitmeyer, 1978). In contrast, at the 34 ms exposure duration (Fig. 5a, right column), no end-stopping is evident when the end-zone masks have the same onset as the target and the center mask (0 ms SOA). Moreover, at longer SOAs, thresholds are generally higher than the baseline value. This suppression is most significant for observer LC whose results show especially strong suppression at positive SOAs, resulting in an asymmetry in the mean curve.

Results obtained at 8.0 cpd (Fig. 5b) are similar to, but weaker than, those at 1.7 cpd. At a 150 ms exposure duration, the end-stopping effect is evident when the end-zone masks have the same or near onset as the target and the center mask (Fig. 5b, left column). However, end-stopping disappears when the exposure duration is reduced to 34 ms (Fig. 5b, right column). In both cases little suppression is shown at longer SOAs, except for LC whose results indicate some suppression at positive SOAs at both spatial frequencies.

These results show that an onset asynchrony of the end-zone masks, whether earlier or later than the center mask, only weakens the end-stopping effect. Giving sufficient exposure time, end-stopping is maximal when

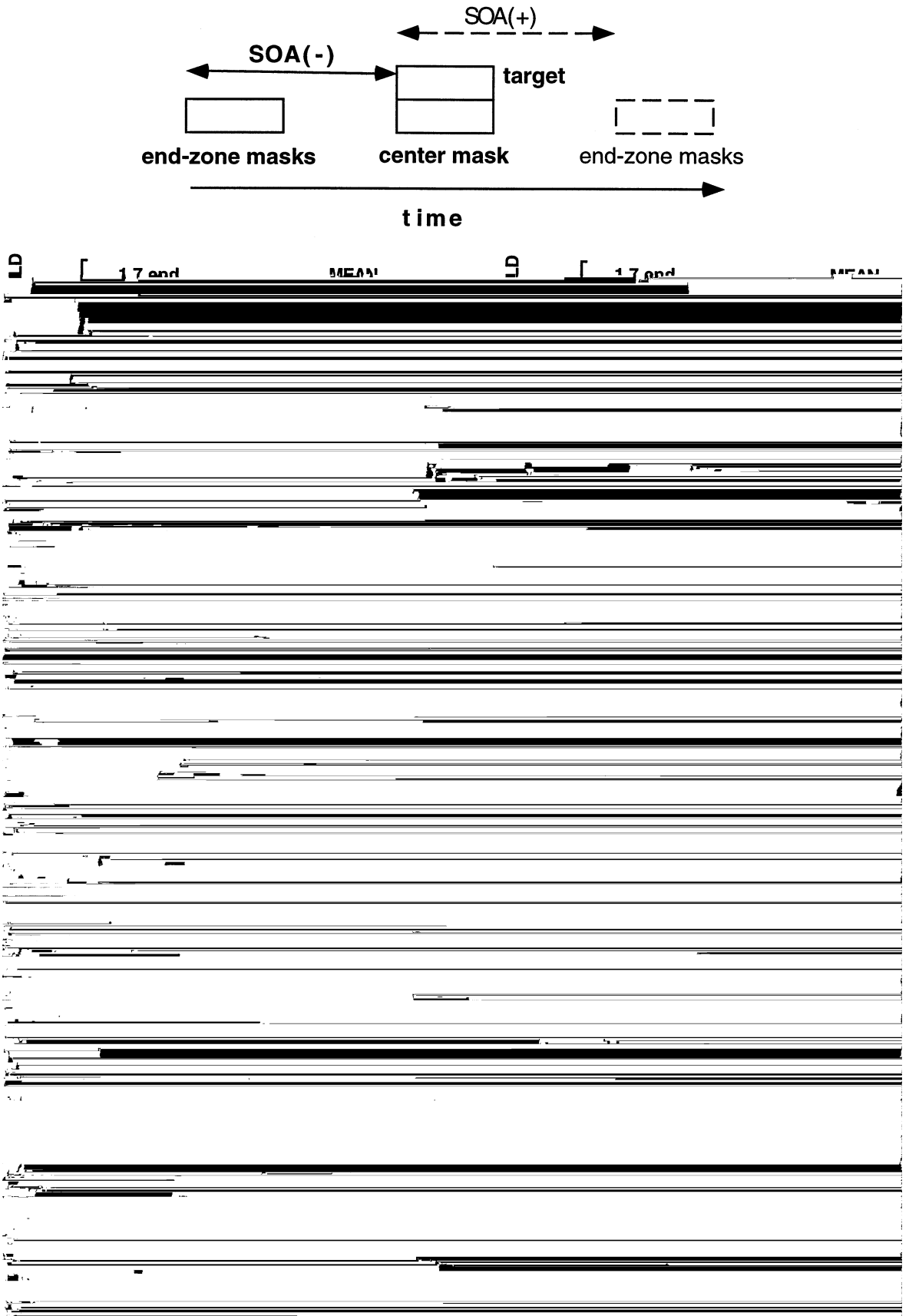

Fig. 5. The effects of SOA between the end-zone masks and the target/center-mask combination on psychophysical end-stopping at short (34 ms) and long (150 ms) exposure durations. (a) The top panel shows the temporal profile of the stimuli. Negative and positive SOA values indicate earlier and later onset of the end-zone masks, respectively. The bottom panels show mean and individual results at 1.7 cpd. Baselines (dashed lines) indicate contrast thresholds measured with no end-zone mask presentation (center mask only). (b) Mean and individual results at 8.0 cpd.

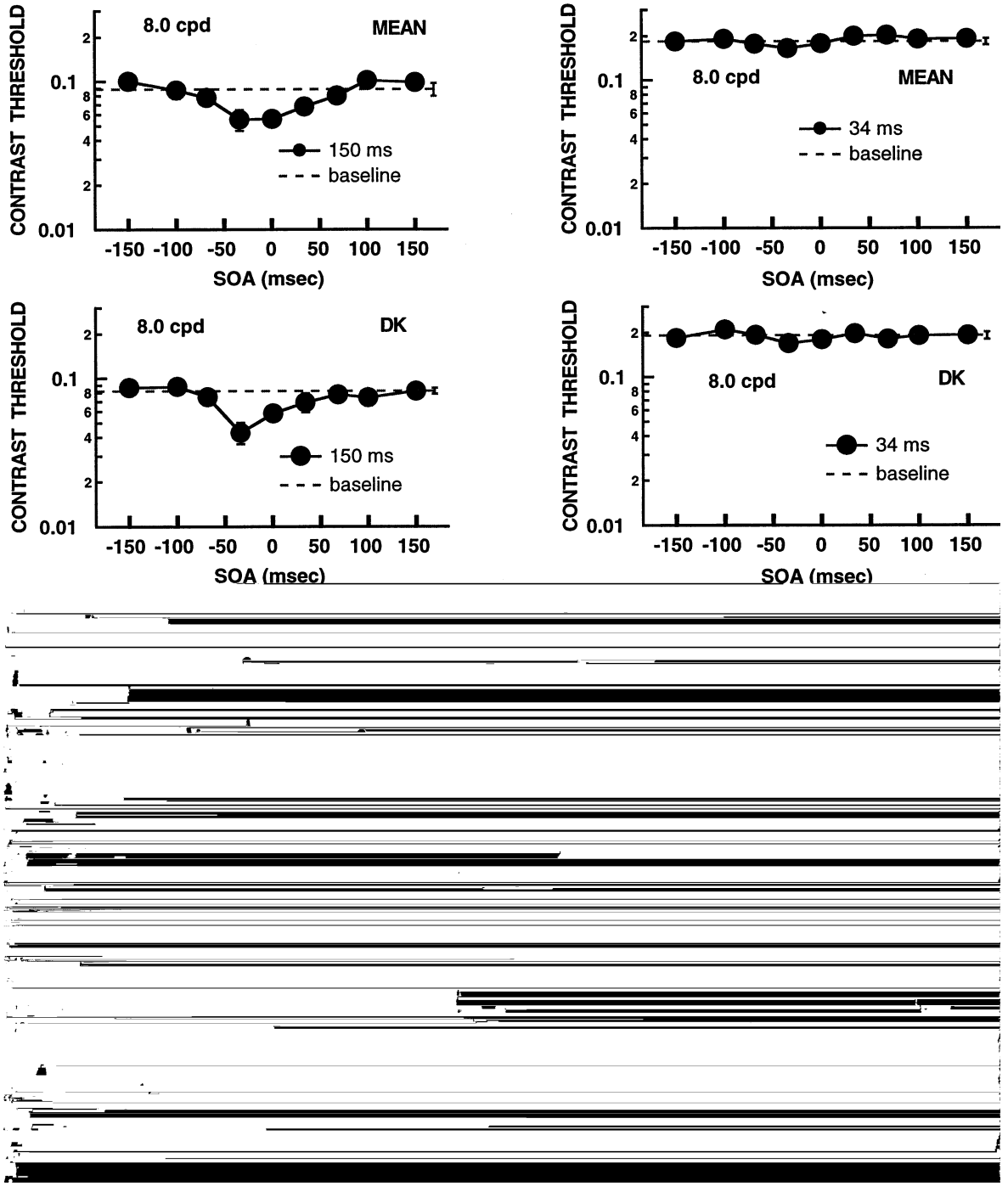

Fig. 5. (*Continued*)

the end-zone masks have full temporal overlap with the center mask. A plausible explanation, which is consistent with neurophysiological findings, is that the neural feedback circuitry which generates psychophysical end-stopping as a result of end-zone masking, is triggered by the activation of the spatial filter center due to center masking. If the center mask and the end-zone masks are insufficiently temporally overlapped because of the stimulus onset asynchrony, as in the above 150 ms condition, or if they are fully temporally overlapped but don't have sufficient exposure duration, as in the 34 ms condition, the re-entrant end-stopping signals simply don't have enough time to reach the spatial filter center and thus have little effect on center masking.

4. Discussion

Acknowledgements

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