Neuronal correlates of visibility and invisibility in the primate visual system

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A brief visual target stimulus may be rendered invisible if it is immediately preceded or followed by another stimulus. This class of illusions, known as visual masking, may allow insights into the neural mechanisms that underlie visual perception. We have therefore explored the temporal characteristics of masking illusions in humans, and compared them with corresponding neuronal responses in the primary visual cortex of awake and anesthetized monkeys. Stimulus parameters that in humans produce forward masking (in which the mask precedes the target) suppress the transient on-response to the target in monkey visual cortex. Those that produce backward masking (in which the mask comes after the target) inhibit the transient after-discharge, the excitatory response that occurs just after the disappearance of the target. These results suggest that, for targets that can be masked (those of short duration), the transient neuronal responses associated with onset and turning off of the target may be important in its visibility.

What makes a stimulus visible? One might think that a pattern of light on the retina should be adequate to generate a visible image, but briefly displayed visual stimuli that are visible when presented alone can be rendered less visible or invisible if preceded or followed by another stimulus. This phenomenon, known as visual masking, was first described 130 years ago[1,2]. Many different types of visual masking effects have been described since then[1,3–6], but although the neural basis of some of these illusions has been examined[6–10], others remain mysterious. We have concentrated here on one of the most interesting visual-masking illusions, in which targets are rendered less visible by masks that are separated from them both spatially and temporally (i.e. when the mask precedes or follows the target, historically called para- and meta-contrast masking respectively[4,5,11]). Here we use these effects to explore the nature of visibility, by correlating those conditions that lead to decreased visibility in humans with the physiological responses to these stimuli in monkey primary visual cortex. Our results indicate that specific parts of the response to a stimulus, the transient onset-response and the after-discharge, are important to the visibility of that stimulus, as inhibition of either of these response components correlates with decreased visibility.

Results

Human perception of visual masking

For the purposes of visual-masking experiments, a target or mask can be almost any stimulus: here we use either black or white bars for both targets and masks (Fig. 1a). Varying the relative timing of target and mask presentation can affect the visibility of the target. Stimulus timing conditions in visual masking can therefore be grouped into three categories: forward, simultaneous, and backward[4,5]. Backward-masking illusions are of special interest because in these conditions a target is rendered invisible by mask-evoked activity that enters the nervous system later in time.

Previous perceptual studies have shown that with backward masking there is a point of minimum visibility that occurs at some particular delay between target and mask[12–17]. These studies, however, did not take into account the possible effects of varying target and mask duration, and so they might have failed to notice some temporal relationships relevant to target visibility. We therefore tested the effect of systematically varying the durations of both targets and masks as well as their relative onset (and hence termination) times, in order to determine which parameters are important for target visibility (see Fig. 1b).

Our stimuli consisted of a pair of isolated bars (targets), each flanked by two non-overlapping bars (masks). The backward masking test was a two-alternative forced choice in which subjects were required to identify the longer bar. We did not use target detectability as an assay because we needed to work with stimuli of suprathreshold brightness for the subsequent physiological experiments. Figure 2 shows the performance of 25 human subjects, plotted as a function of stimulus-onset asynchrony (SOA, the interval between the onset of the target and the mask), inter-stimulus interval (ISI, the interval between the termination of the target and the onset of the mask) or stimulus-termination asynchrony (STA, the interval between the termination of the target and of the mask). Figure 2a shows performance as a function of stimulus-onset asynchrony. The point of maximum backward masking (drop lines) does not occur at a constant SOA, but rather varies for different mask and target durations. As shown in Fig. 2d, there is a trend (shown here using the data from when the mask was 50 milliseconds in duration) for optimum backward masking to occur at later times for longer target durations, suggesting that it is the termination of the target that correlates with the timing of maximum backward masking (slope of linear regression, 0.98 ± 0.06, $p<0.01$). The data were therefore replotted as a function of the inter-stimulus interval (Figs. 2b and 1b). The times of peak masking then fell into two groups

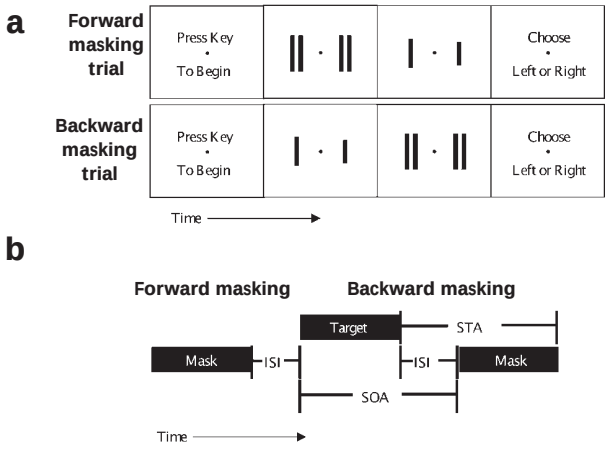

Fig. 1. Experimental design. **(a)** The sequence of events during the course of a trial. The trial started with a delay of 500 to 1500 ms. In backward-masking conditions, the target was presented, followed by the mask. In forward-masking conditions, masks came before targets. After termination of the second stimulus (mask or target), there was another 500-ms delay, after which the subject indicated which side had the longer target. **(b)** A schematic view of the various timing parameters used in these experiments. SOA, stimulus onset asynchrony, the interval between the onset of target and of mask; STA, stimulus termination asynchrony, the interval between termination of target and of mask; ISI, inter-stimulus interval, the interval between the termination of the target and the onset of the mask (backward masking) or between the termination of the mask and the onset of the target (forward masking).

corresponding to the two mask durations tested. The fact that maximum backward masking occurred at shorter inter-stimulus intervals for longer duration masks implies that mask termination produces a particularly strong masking effect. When the data were replotted as a function of stimulus termination asynchrony (Fig. 2c; see also Fig. 1b), the points of maximum masking clustered around a stimulus-termination asynchrony of about 100 milliseconds. Therefore STA is the best descriptor of the time of peak backward masking, as the dispersion of the peak masking times was lowest when plotted on the STA scale (Fig. 2e; Bartlett's test, $p<0.01$).

Theoretical models of backward masking that predict optimum masking at a particular stimulus-onset asynchrony are therefore probably incorrect. Previous studies confounded SOA, ISI and STA by failing to vary systematically both target and mask durations.

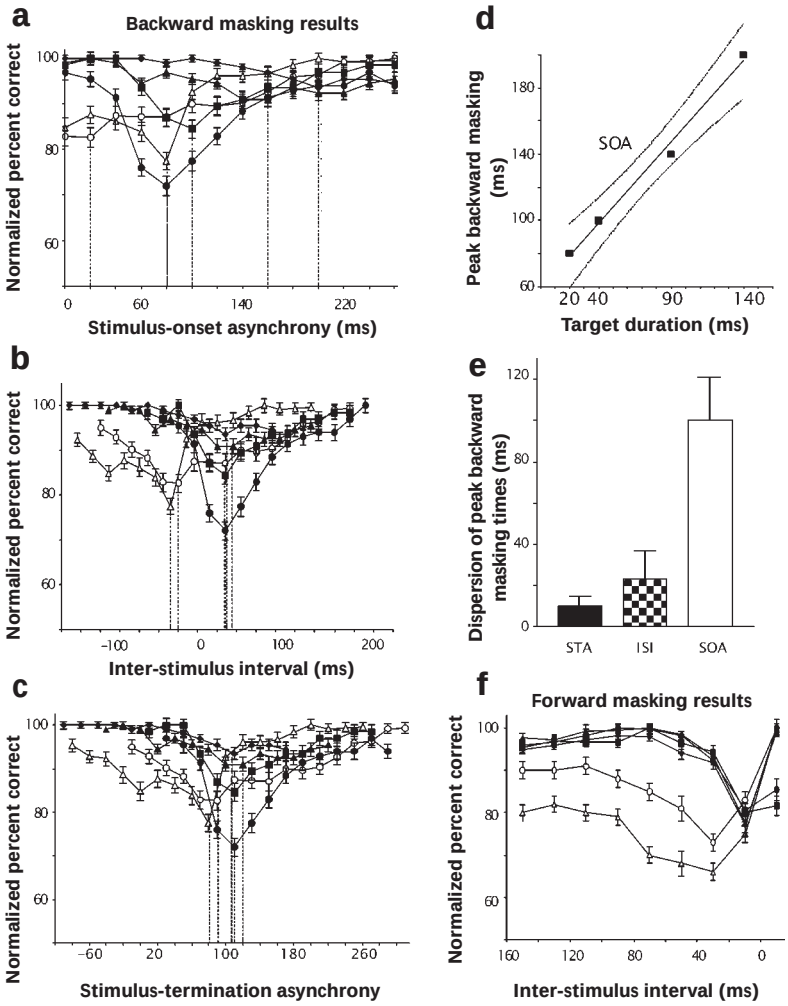

Fig. 2. Psychophysical measurements of the timing parameters important for visual masking. 'T' represents the duration (in milliseconds) of the target, and 'M' represents the duration of the mask. Average for 25 subjects are shown. **(a)** Results from backward-masking conditions plotted on a stimulus-onset asynchrony scale. Note that the points of peak masking (the x-intercepts of the drop-lines) are widely dispersed. (P) T=20, M=50. (L) T=40, M=50. (G) T=90, M=50. (R T=140, M=50. (p) T=20, M=90. (g) T=90, M=90. **(b)** Results from (a) replotted here as a function of inter-stimulus interval. The points of peak masking tend to cluster in two places, correlated with mask duration (open symbols versus closed symbols). **(c)** Results from (a) replotted here on a stimulus-termination asynchrony scale. The points of maximal masking are no longer dispersed, and instead cluster around an STA of about 100 ± 20 ms. **(d)** Linear regression (with 95% confidence intervals) of peak backward-masking times in terms of SOA when the mask was 50 ms in duration. **(e)** The amount of dispersion of peak backward masking times for data tested against stimulus termination asynchrony, inter-stimulus interval, and stimulus onset asynchrony. Notice that the peak backward-masking times are least dispersed on an STA scale, and so STA is the best predictor of backward masking. **(f)** Results from forward-masking conditions; the optimal predictor of peak masking was the inter-stimulus interval between the termination of the mask and the onset of the target.

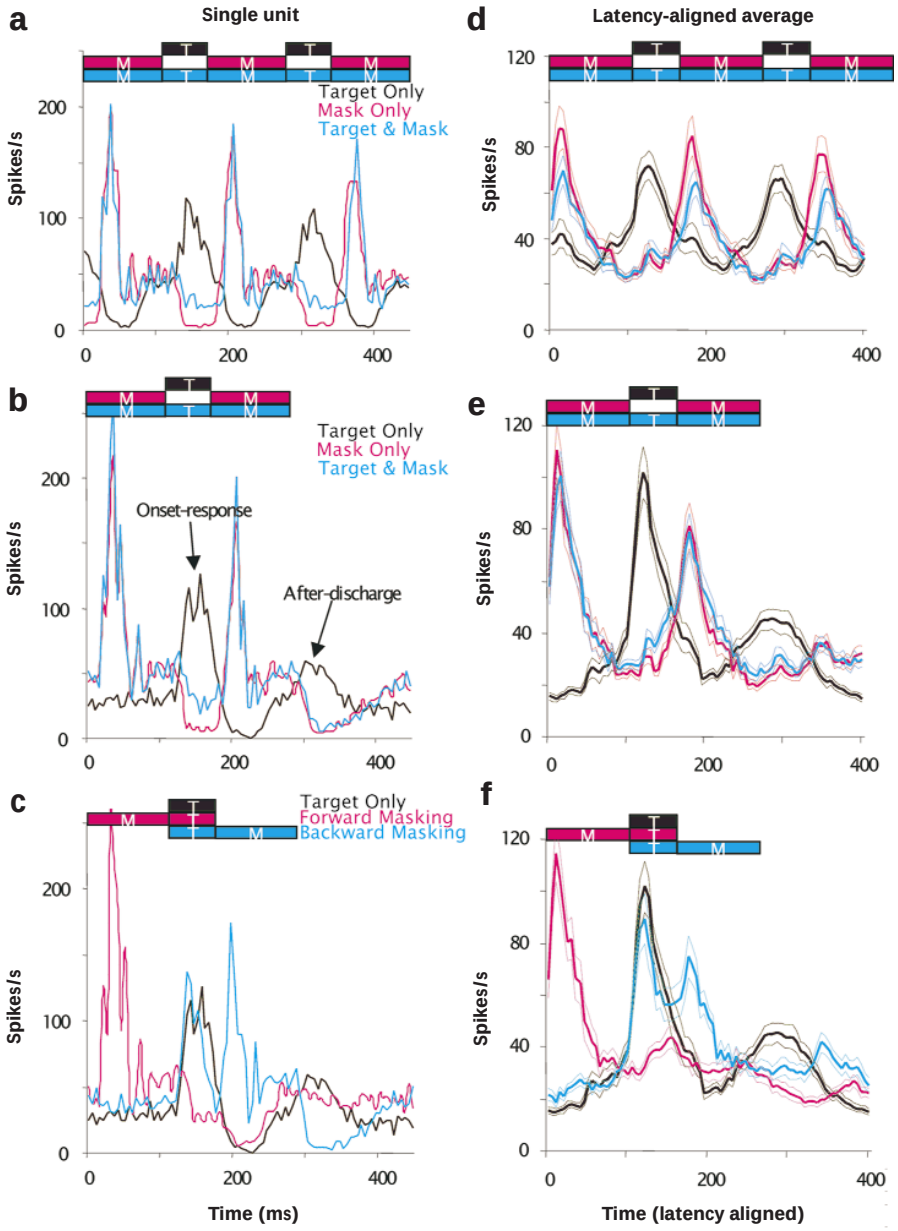

Fig. 3. Individual (a–c) and averaged (d–f) responses of 30 neurons in area V-1 of alert rhesus monkey, plotted with 5-ms bin width. Each cell was tested with at least 50 stimulus presentations for each condition. For averaging across cells, individual neurons with different response latencies were aligned by their half-maximal responses to the mask[30]. The colored bars above each graph represent the time-course of the stimuli. The top panels **(a, d)** show responses to the Standing Wave of Invisibility illusion. The black line represents the response to the target alone. The pink line represents the response to the mask alone. The blue line represents the illusion condition in which the target and mask were presented together and the target appeared to be invisible. The center panels **(b, e)** are similar to those above except that each target-mask-target sequence is separated from the next by a 200-msec pause to reveal onset- and termination-associated responses. The bottom panels **(c, f)** show the target-only data from the center row (black) and the effect of adding only a forward mask (pink line) or backward mask (blue line). The dotted lines in the averaged histograms refer to the standard error of the mean of all cells.

Some previous visual masking studies have varied either target or mask duration, but never both[18–20]. They reported that mask or target duration modulated the apparent brightness of targets, but did not discuss the effect of target or mask duration on the timing of peak visual masking. Nevertheless, the figures published from these earlier studies do show a trend consistent with our findings.

We next tested forward-masking conditions in 20 subjects with the same methods used for backward masking (Figs. 2f and 1b). Previous studies have suggested that forward masking is best described as a function of inter-stimulus interval[9,10]. Our studies confirm this and strengthen it by systematically varying both target and mask duration. Linear-regression analysis shows that the time of maximum forward masking varies linearly as a function of mask duration (slope, -1.5 ± 0.02, $p<0.01$). This implies that maximum forward masking correlates best with the delay between the end of the mask and the onset of the target (ISI, 20 ± 10 ms), and therefore shows least dispersion when plotted as a function of ISI, rather than of SOA or STA (Bartlett's test, $p< 0.02$).

To summarize the psychophysical results, backward masking was strongest when the mask was turned off about 100 milliseconds after the target was turned off (STA, 100 ms), and forward masking was strongest when the mask was turned off immediately before the target was turned on (ISI, 20 ms).

From these observations, we created a new illusion designed to maximize both forward and backward masking. A target of 60-milliseconds duration flickered cyclically in alternation with a spatially non-overlapping mask of 110 milliseconds duration, so that there was always either a mask or a target, but never both, on the screen. In this illusion the target is continuously masked to most viewers. This very strong masking illusion, which we call the Standing Wave of Invisibility, probably occurs because every occurrence of the mask strongly forward-masks the subsequent target (as the mask

turned off just as the next target turned on) and strongly backward-masks the previous target (as the mask also turned off 110 milliseconds after the previous target turned off). This illusion can be seen on the worldwide web at http://cortex.med.harvard.edu/~macknik/standingwave.html.

Neural correlates of visual masking

We sought clues to the neurophysiological basis of masking illusions in the primary visual cortex, area V-1, of awake behaving rhesus monkeys using methods described elsewhere[21,22]. We chose to examine these effects in primates because the psychophysics of visual masking in primates is similar if not identical to that of humans[23]. We studied area V-1 because previous psychophysical studies found that perception of a target presented to one eye can be blocked by a mask presented to the other eye[24–27], suggesting that masking is induced in the cortex, where inputs from the two eyes are first combined[39]. First we characterized the receptive field of each single unit (or sometimes multiple-unit activity), with a combination of hand mapping and eye-position-corrected, reverse-correlation methods[21,22]. We then presented the Standing Wave of Invisibility illusion, with two flanking mask bars directly abutting the target. (This configuration generates strong and constant perceptual masking in humans.) The target bar was centered on the receptive field in the preferred orientation; because the mask was very close to the target, it also overlapped the receptive field in many cases. We recorded responses either to the illusory condition (target plus mask in counter-phase) or to the target and mask separately. As shown in Fig. 3a, the response to the target alone (black line) is inhibited when the mask is presented in counter-phase (blue line), the condition in which the target appears less visible to human observers. Twenty-three out of thirty V-1 cells (77%) showed this inhibition ($p \leq 0.05$; two-tailed t-test). Figure 3d shows the average over all 30 cells. In order to average across cells with different latencies, the traces were aligned by their half-maximal responses to the mask. The predominant effect was an inhibition of the target response in the masked condition ($p<0.01$).

The psychophysical results in Fig. 2 suggested that neural events correlated with the target's onset might be particularly important to its visibility, because in the forward-masking condition, visibility depended on the interval between the termination of the mask and the onset of the target. The results of the backward-masking condition further suggested that neural events correlated with the termination of the target might also be important; visibility depended on the interval between termination of the target and of the mask. We therefore examined the transient responses to the onset and termination of the target by using conditions in which the target was displayed with several hundred milliseconds between each presentation. Figure 3b shows the response to one such presentation. When the target was displayed alone, transient responses to both onset and termination could be seen. When each target was both preceded and followed by a mask (when the target appeared less visible) the onset-response from the target was inhibited in 25 out of 30 cells (83%, $p \leq 0.05$) and the after-discharge was inhibited in 24 out of 30 cells (80%; $p \leq 0.05$). In the average of all cells (Fig. 3e), both the target's onset-response and its after-discharge were inhibited ($p<0.01$).

We also tested (Fig. 3c,f) the effect of the forward or backward mask alone (pink and blue lines respectively) on the target's response. Figure 3c (individual neuron) and Fig. 3f (normalized average) show that the effect of the forward mask was to inhibit the target's response almost completely (24 cells out of 30 (80%), $p \leq 0.05$; average, $p<0.01$). The effect of the backward mask was to inhibit selectively the target's after-discharge (22 cells out of 30 (73%), $p \leq 0.05$; average, $p<0.01$). We conclude that both the onset-response and the after-discharge to a stimulus contribute to its perception because inhibition of either can occur under conditions that produce visual masking in humans. The results published from previous physiological studies are consistent with the results we present here[9,10,23,28], though they did not draw any conclusions about the after-discharge. Schiller, for example, in the first single-cell study of masking[10], presented a target and mask with various inter-stimulus intervals. At the inter-stimulus interval corresponding to perceptual masking,

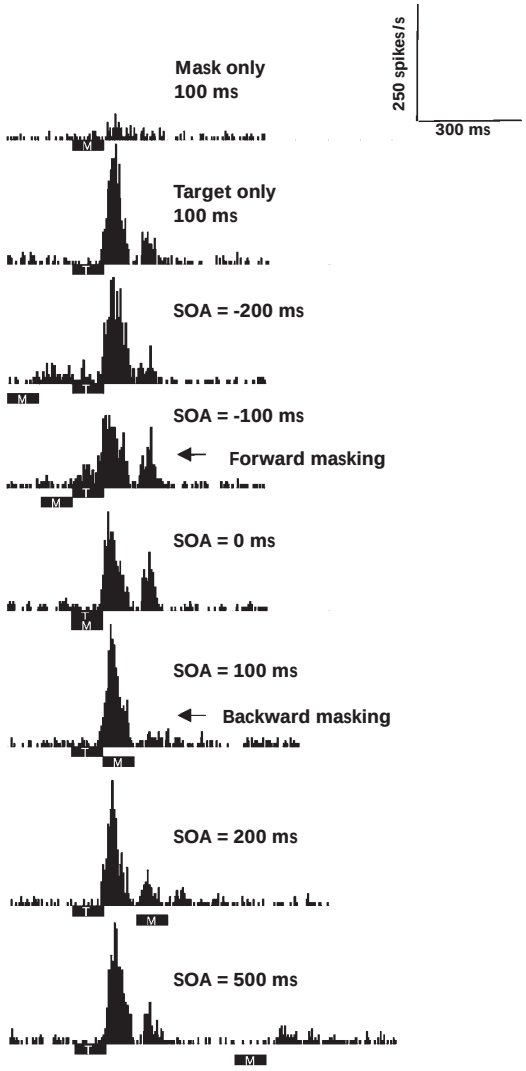

Fig. 4. Multi-unit recording from upper layers of area V-1 in an anesthetized rhesus monkey. The aggregate receptive field was foveal, 0.1° square, and well oriented. In contrast to the recordings from alert animals, the mask is largely outside the receptive field. Black boxes below each histogram represent the time course of the mask (M) and target (T). Notice that under conditions that best correlate with human forward masking (ISI of 0 ms, here corresponding to SOA of -100 ms), the main effect of the mask is to inhibit the transient onset-response to the target. Similarly, in the condition that produces maximum backward masking in humans (STA of 100 ms, here corresponding to SOA of 100 ms), the after-discharge is specifically inhibited. Each histogram is an average of 50 trials with a bin width of 5 ms.

the after-discharge to the target seems to be selectively inhibited.

Although our results indicate the importance of the transient onset-response and the after-discharge, it is unclear how inhibition of the sustained portion of the response would affect the visibility of the target. In awake-monkey experiments, the sustained portion of the target's response was often obscured by the excitatory response from the mask. The mask, in these conditions, was to some degree within the cell's receptive field, and so it often evoked excitatory responses as strong as those to the target itself. We therefore did similar experiments in anesthetized paralyzed monkeys, where the absence of eye movement allows retinal positions of the target and mask to be precisely controlled. We were able to move the mask away from the target and find positions in which it was still inhibitory to the target response yet did not excite the cell. This increase in distance led, however, to more modest levels of inhibition from the mask, just as increased distance is known to lead to decreased perceptual masking[29].

We examined the pattern of responses evoked in 153 cells in the primary visual cortex of anesthetized macaque and squirrel monkeys (10 squirrel, 2 cynomologous and 1 rhesus). The results from anesthetized animals (Fig. 4) complement the results from awake animals; under forward-masking conditions, the target's transient onset-response was inhibited, and under backward-masking conditions, the target after-discharge was inhibited. We also examined the effects of masks on the response to longer presentation of the target (334 ms), as this allowed us to examine the effects on the sustained phase of the response as well as the onset- and termination-associated responses. We found that the mask could inhibit the sustained part of the target response as well as the transient parts (Fig. 5). These stimulus conditions are not directly comparable to human psychophysics because using anesthetized paralyzed animals is equivalent to using retinal stabilization in humans, which has not been done in studies of masking illusions. These results nevertheless suggest that if the sustained parts of the response were as important to visibility as the transient parts, visual masking would occur at intervals that produce sustained response inhibition, and they do not. We therefore suspect that sustained portions of response are less important than transient responses in determining visibility of targets. This may reflect the fact that sustained responses in awake animals are smaller than transient responses[30].

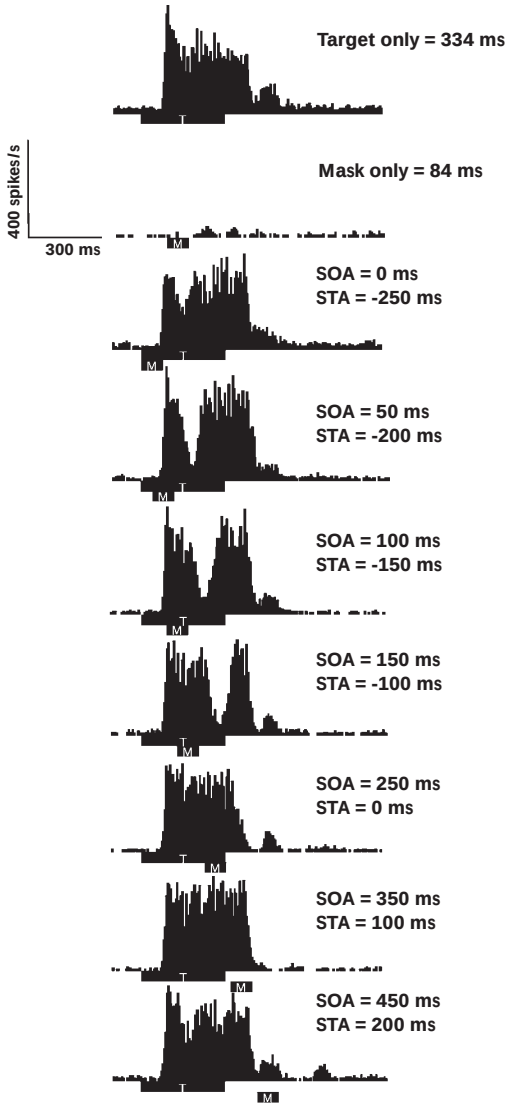

Fig. 5. A multi-unit recording from layer 4B of an anesthetized squirrel monkey, showing responses to a longer-duration target (target duration, 334 msec; mask duration, 84 msec). The aggregate receptive field was 0.5° square, and the masks were presented at a distance of 3° to either side. Traces represent the cells' response to target alone (top trace), mask alone (second trace), or both (all other traces). The inhibitory effect of the mask is evident at all SOA values. Each histogram represents the average of 50 trials.

Discussion

Our forward-masking experiments in human subjects show that the degree of masking depends on the interval between the termination of the mask and the onset of the target, suggesting that there is something about the target's onset that is important to its visibility. The degree of backward masking depends on the interval between the termination of the target and the termination of the mask, suggesting that termination-associated responses are also important to visibility. Specifically, terminating a mask about 100 milliseconds after a target has been terminated results in strong masking, suggesting that something important for target visibility occurs about 100 milliseconds after it has been extinguished. Consistent with these psychophysical observations, the strongest responses to a target are associated with its appearance and disappearance, in the form of an onset response and after-discharge. By recreating visual masking conditions during physiological recordings in monkeys, we have found that the stimulus parameters that cause decreased target visibility in humans also result in inhibition of either the transient onset response or the after-discharge in primary visual cortical neurons.

The observation that inhibition of the transient onset response correlates with a reduction in target visibility fits with conclusions by others that it is the earliest spikes in a stimulus-evoked response that are the most important for neural information processing[31,32]. It has been suggested that bursts of spikes may carry more information than steady firing[21,33]. It is somewhat counterintuitive, however, that the after-discharge contributes to target visibility, as stable real-world objects do not turn off and should therefore not generate after-discharges. However, the eyes, when open, are rarely stationary[34], so real-world stimuli actually do turn on and off several times per second from the point of view of visual receptive fields. If images are experimentally stabilized on the retina, they fade[35–37]; indeed, Coppola & Purves[37] showed that a stabilized image fades in as little as 80 milliseconds, consistent with the idea that the initial

onset-response can produce only a transient visible image. Moreover, Yarbus[34] showed that retinally stabilized images that had faded from view would reappear as a positive image after the stabilized image was turned off, consistent with our suggestion that the after-discharge also contributes to visibility. We therefore conclude that transient phases of visual responses, both onset responses and after-discharges, may be particularly important to visibility.

Methods

STIMULI. Stimuli in the psychophysical and physiological experiments were presented on a NEC 5FG monitor at a refresh rate of 100 Hz. The monitor subtended 32° by 25° at a viewing distance of 58.5 cm. In the human psychophysical experiments, each trial's stimulus consisted of one to three 0.5° vertical bars on the left, and corresponding bars on the right with a 0.2°-wide circular dot in the center of the screen that served as a fixation point. All stimuli were black against a background of 18% contrast white (CIE x = 0.333, y = 0.333, 26.74 lumens) in a dimly lit room.

In the physiological experiments, the dimensions of the target (a single oriented bar with optimal contrast to the background, either black or white) were optimized for each cell. Masks were given the same characteristics as the targets in the human experiments, and they also flanked, but did not spatially overlap, the targets.

PROCEDURE. In the human psychophysical experiments, the targets were vertically oriented bars of different lengths and 0.5° width that were placed 3° to the right and left of the fixation point. The left side of the subject's screen matched the right side in every way except for the height of the target. The two possible combinations of target length on the screen at any given time were either 4° and 4.5°, or 4.5° and 5°. By using only one of these sets of targets in a given trial (and by randomly placing each set within the block of trials), we were able to ensure that the subject did not use local retinal cues to learn the appropriate target lengths, especially as the 4.5° high bar was the longer bar in one set, but was the shorter in the other. Subjects could not, for instance, simply remember the height of the long target compared to its neighboring mask in one trial and use visual memory to choose the long target in the next trial; they had to actively compare each target each trial in order to choose correctly. The duration of the targets was varied. The masks were bars 0.5° wide and 6° high that flanked the targets on either one or both sides. Target duration, mask duration and their relative onset times were varied parametrically.

In the physiological experiments, standard electrophysiological techniques for recording from anesthetized paralyzed animals were used[38]. Previously published techniques were also used in the awake behaving primate experimental procedures[21,22].

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