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Masking Interrupts Figure–Ground Signals in V1

Victor A. F. Lamme[1], Karl Zipser[2], and Henk Spekreijse[3]

Abstract

■ In a backward masking paradigm, a target stimulus is rapidly (<100 msec) followed by a second stimulus. This typically results in a dramatic decrease in the visibility of the target stimulus. It has been shown that masking reduces responses in V1. It is not known, however, which process in V1 is affected by the mask. In the past, we have shown that in V1, modulations of neural activity that are specifically related to figure–ground segregation can be recorded. Here, we recorded from awake macaque monkeys, engaged in a task where they had to detect figures from background in a pattern backward masking paradigm. We show that the V1 figure–ground signals are selectively and fully suppressed at target–mask intervals that psychophysically result in the target being invisible. Initial response transients, signalling the features that make up the scene, are not affected. As figure–ground modulations depend on feedback from extrastriate areas, these results suggest that masking selectively interrupts the recurrent interactions between V1 and higher visual areas. ■

INTRODUCTION

When a visual stimulus is rapidly followed by another one, the visibility of the first stimulus may be greatly reduced, depending on factors like relative timing (stimulus onset asynchrony [SOA]), similarity, and spatial position of the two stimuli (Enns & DiLollo, 2000; Breitmeyer, 1984). This phenomenon is known as backward masking. Masking is not simply due to the fact that the first stimulus is presented briefly. Stimuli presented for only several milliseconds are still clearly visible when they are not followed by another stimulus. However, in a masking experiment with an SOA of, say, 50 msec, we do not, as might be expected, perceive the first stimulus for 50 msec and then the second one after that. Rather, under appropriate conditions, the first stimulus may not be visible at all. Backward masking thus reveals an important temporal nonlinearity of visual perception.

There are two general classes of models to explain backward masking. Feedforward inhibitory models explain backward masking by asserting that the second stimulus exerts an inhibitory influence on the neural signal that is evoked by the first stimulus. This inhibition is postulated to occur at levels of processing before stimuli are fully categorized and made available to conscious recognition systems. In other words, the second stimulus somehow catches up with the first one before it reaches a conscious level (Breitmeyer, 1984). Another type of models argues that masking interferes with so-called reentrant or recurrent processing. In recurrent processing, information flows from low to high levels, and then back again to the low levels (and this may occur several times). Only when the latter condition is met, stimuli are sufficiently processed to allow for conscious recognition (Lamme 2000; Lamme & Roelfsema 2000). In these models, masking interrupts recurrent processing, because by the time the high-level signals reach the lower levels, information at these lower levels is not about the first stimulus, but about the second one, the mask (Enns & DiLollo, 2000).

Previous studies on the neurophysiological events during masking have not been able to discriminate between the two alternative hypotheses. In early visual areas, such as V1, backward masking typically has no effect on the early components of neural responses. In fact, the temporal order of neural responses is mostly a reflection of the temporal order of stimulus and mask (Macknik & Livingstone, 1998; Bridgeman, 1980). If it were assumed that the activity in these early visual areas is not available to consciousness, this can be taken as evidence for either of the two hypotheses. However, in higher visual areas, such as IT, which are often assumed to be closer to the conscious level of visual processing, more or less the same result is obtained; early transients are not affected by subsequent masks (unless SOAs get very short) (Kovacs, Vogels, & Orban, 1995; Rolls & Tovee, 1994). It seems, therefore, that a mask never really "catches up" with the first stimulus in the sense of the feedforward inhibitory model, not even in the highest visual areas. However, masking does have another effect on the responses of IT neurons; Rolls, Tovee, and Panzeri (1999) calculated the amount of information about the first stimulus that remains in the neurons' signals at various masking SOAs. At short SOAs, there

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was less information about the first stimulus than at longer SOAs. The amount of ''neural'' information was a good predictor for the strength of the psychophysical masking effect. But again, this would be compatible with both feedforward and recurrent models.

Here, we study the effect of pattern backward masking on neural activity in V1. This has been studied before, and it was found that backward masking (at SOAs of, say, 40 msec) has little effect on the early transient response that is evoked by the first stimulus. The mask mostly interferes with the neural response at some delay, usually comparable to the delay between stimulus and mask (Macknik & Livingstone, 1998; Bridgeman, 1980). For example, in V1, a stimulus will evoke a response starting at 40 msec after its presentation due to the processing and conduction in the retino-geniculo-striate pathway. When a mask follows this stimulus at 50 msec, the effect

of this mask is typically expressed at 50 + 40 = 90 msec. It is not clear, however, which process is influenced at these latencies. We build on findings showing that in V1, at shorter latencies (∼55 msec), the orientation of line elements are detected, while at longer latencies (∼100 msec), the V1 neurons signal the difference between textured figures and background (Figure 1) (Lamme, Rodriguez, & Spekreijse, 1999). Orientation selectivity has been shown to depend almost exclusively on feedforward mechanisms (Das, 1996; Ferster, Chung, & Wheat, 1996). The delayed figure–ground signals, on the other hand, most likely are a manifestation of recurrent processing, involving horizontal connections and extrastriate areas (Lamme, Supèr, & Spekreijse, 1998a; Lamme, Zipser, & Spekreijse, 1998b). We determine which of these two processes are affected by masks at SOAs that result in reduced visibility of the stimuli.

We presented textured figure–ground displays with the figure either on the left or the right side of the fixation spot. These displays were shown for 1 to 8 monitor frames (14–110 msec) and were then followed by a texture pattern mask. We trained monkeys to report whether they perceived the masked figures by making a saccadic eye movement towards the figure. Meanwhile, we recorded neural activity from neurons in V1 (Figure 2).
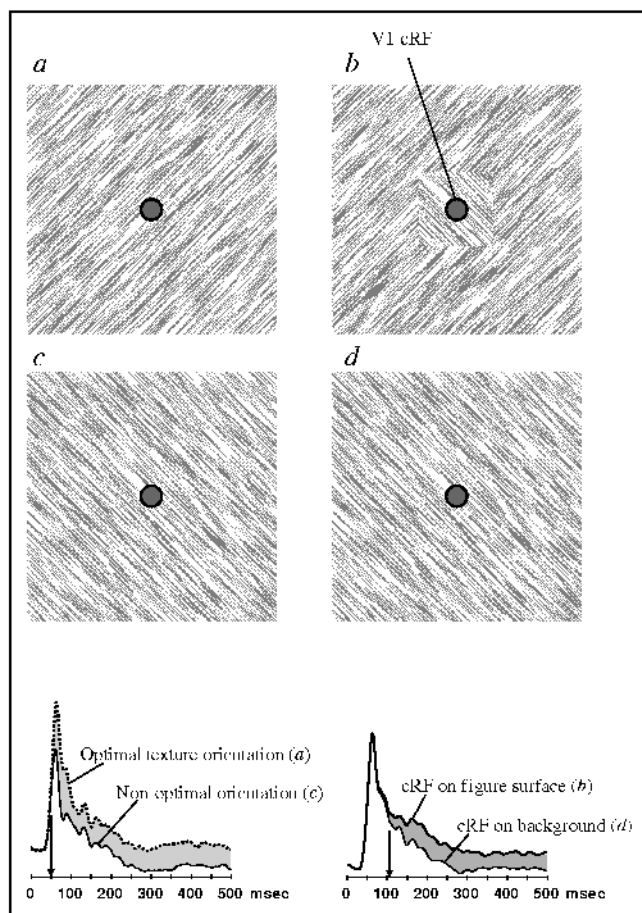

Figure 1. V1 cells are sequentially selective for various aspects of a stimulus. Responses are compared with receptive fields of V1 neurons (V1 cRF) overlaid by different (a–d) textured scenes. Comparing a with c (left graphs, gray shading indicates difference) shows that cells are selective for the orientation of textures at 55 msec (arrow indicates moment of first significant difference). When responses to situation b and d are compared (right graphs), the stimuli within the RF are identical. Nevertheless, responses to the figure texture are stronger than to background texture, starting at a latency of 100 msec, indicating that at this latency, neurons signal figure–ground relationships. Stimulus onset is at 0 msec.

RESULTS

Texture Pattern Masking Leads to Reduced Visibility of Textured Figures

When the figure–ground stimuli were followed by the texture pattern masks, at short SOAs, the monkeys were at chance in detecting the position of the figures. At longer SOAs, the monkeys could very reliably (∼90% correct) detect where the figure was presented (Figure 3 top). This ''classical'' dependency on SOA indicates that the pattern masks were effective in masking the figure–ground displays. The performance of the two monkeys was very similar. Therefore, we are, from now on, considering the results of the two animals pooled together (Figure 3 bottom). That the masking is due to the presentation of the patterns masks, and not due to the short presentation of the stimuli per se, is indicated by the fact that short stimulus presentations followed by a blank screen do not result in effective masking (Figure 3 bottom). Texture pattern masks are thus producing effective backward masking of textured figure–ground displays.
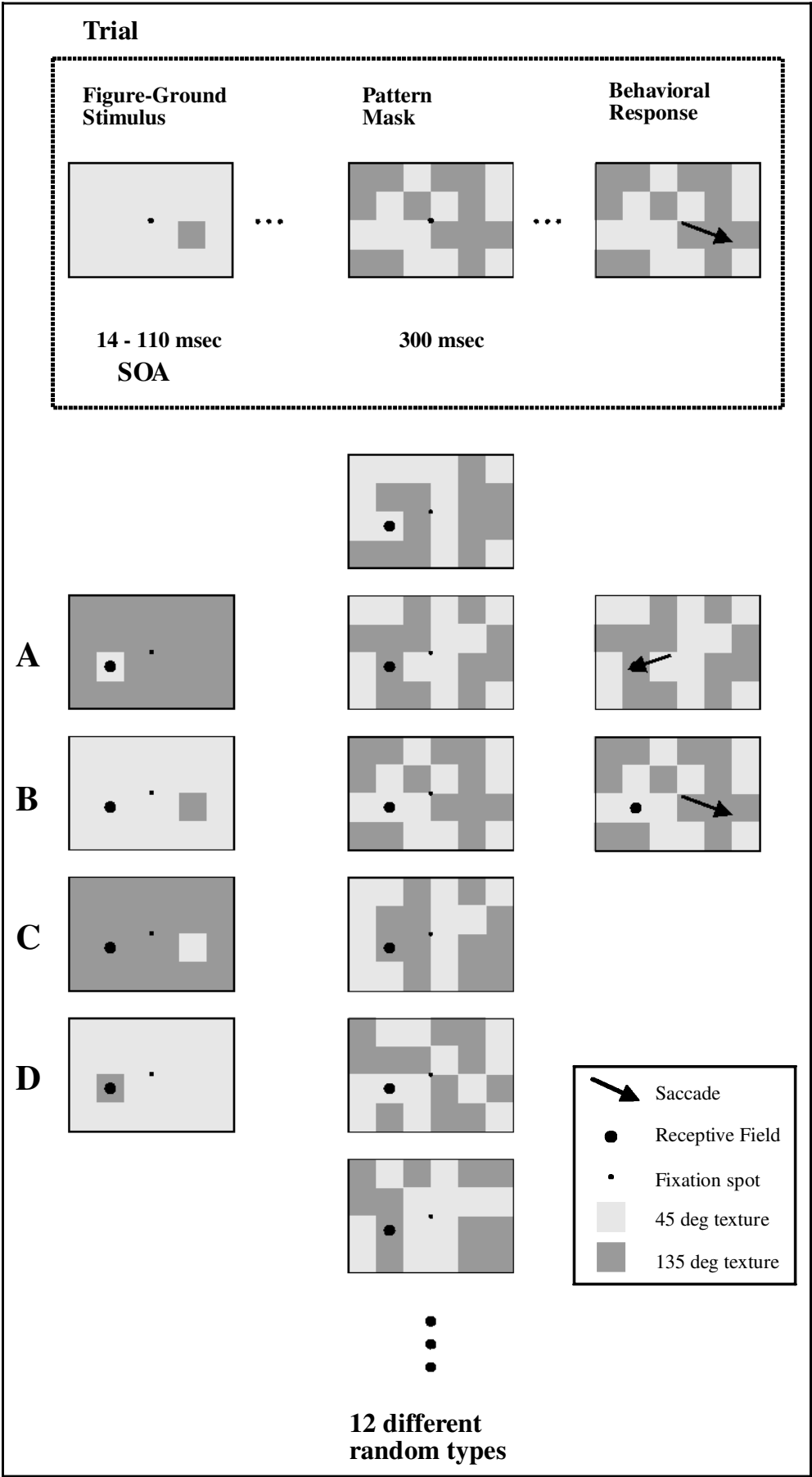
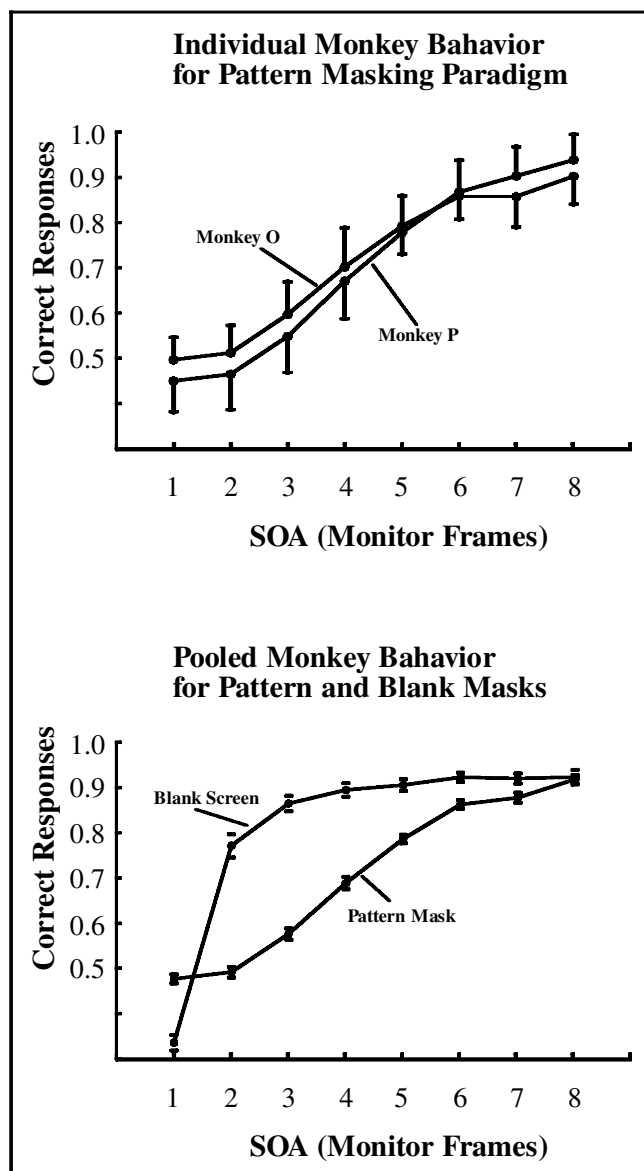### Texture Pattern Masking Leads to a Suppression of Figure–Ground Modulation

Figure–ground modulation is the difference between neural activity evoked by texture elements that belong to a figure and activity evoked by the same elements of

Figure 2. Stimulus paradigm. A trial (top box) consists of the presentation of a figure–ground display, followed within 14–110 msec (the SOA) by a textured mask. The required behavioral response is a saccade to the position of the figure in the first (figure–ground) display. At stimulus onset (0 msec), one of four (A to D) textured scenes appears, containing a figure on a background (left column). After the SOA (14–110 msec), this scene is followed by 1 of 12 different textured pattern masks (center column). After 300 msec of fixation, the animal is allowed to make an eye movement to the original position of the figure in the figure–ground display (right column), while the mask stays on display. See figure for legend.

Trial

Figure-Ground Stimulus   **Pattern Mask**   **Behavioral Response**

14 - 110 msec SOA   **300 msec**

A

B

C

D

Saccade
Receptive Field
Fixation spot
45 deg texture
135 deg texture

12 different random types

Figure 3. Behavioral results. Top: Percentage correct responses (i.e., saccades towards the figure position), with respect to SOA between figure–ground display and pattern mask, for the two animals O and P. Error bars denote standard deviation. Bottom: Two monkeys' average performance for the pattern mask condition and the blank screen condition, where the figure–ground display is followed by a blank screen instead of a mask. Error bars denote standard error of mean. For both conditions, chance level is 50%.

the background (Lamme, 1995). Therefore, we compared the average response to Stimuli A and D with the average response evoked by Stimuli B and C (see Figure 2 and Methods). From the point of view of what is on the receptive field (RF), the two sets of stimuli are identical. Because all types of masks were used in combination with all four (A–D) kinds of stimuli, no difference in neural response is to be expected on that basis between the two sets either. Any difference in response must be due to the neurons signalling the difference between figure elements and background elements, just like what is shown in Figure 1, right.

Figure–ground modulation can still be observed at longer SOAs. At short SOAs, however, the modulation appears to be absent (Figure 4 top). To quantify the amount of modulation at the different SOAs, we calculated, per recording site, the mean level of activity evoked by the two sets of stimuli during the 40-msec interval where modulation is to be expected (we selected this interval based on the population average, so as to capture the maximal amount of modulation in all conditions; see the dotted line in Figure 4 top). The difference between the two sets of responses, that is, figure–ground modulation, shows a clear dependency on SOA (Figure 4 bottom, bars). Significant modulation ($p < .025$) is only found at SOAs of 5, 6, 7, and 8 frames (two-sided t test with the electrodes as a group, t statistics for the 1- to 8-frame conditions: 0.40, 0.13, 0.44, 2.23, 5.21, 4.96, 5.96, 3.17, respectively).

We wanted to compare to what extent this "neurometric" curve corresponds to the psychometric curve from the behavioral results. To do this, we took the maximum amount of modulation (0.18) and equated this to 100% correct performance, and we equated zero modulation to chance performance (Figure 4 bottom, bars vs. line). The mean squared difference between these two measures is 0.033.

Short Stimulus Presentation per se Does Not Lead to Suppression of Figure–Ground Modulation

It might be that the absence of modulation at short SOAs in the pattern masking experiment is simply due to the fact that at these short SOAs, the stimulus is presented too short to evoke modulation. In that case, it would not be a result of backward masking. Therefore, we analyzed to what extent figure–ground modulation is affected by short stimulus presentation that are followed not by a pattern mask but simply by a blank screen. We performed the exact same analyses as we did in the previous section. We found that figure–ground signals are still present at very short SOAs (Figure 5 top). Significant ($p < .025$) modulation is found at all SOAs except that of 1 frame (Figure 5 bottom) (two-sided t test with the electrodes as a group, t statistics for 1- to 8-frame conditions: 0.05, 2.44, 5.32, 4.14, 5.60, 5.65, 3.98, 5.33, respectively). A comparison of the neurometric curve with the psychometric curve, in this case, that of the blank screen experiments (Figure 5 bottom, bars vs. line), again resulted in a close correspondence between the amount of modulation and the behavioral performance of the animals (mean squared difference = 0.036).

Texture Pattern Masking Does Not Lead to a Suppression of Feature Detection

Our paradigm allowed for another analysis on the same set of data. When we compare the responses to Stimuli

A and B to the response to Stimuli C and D, we obtain a measure about to what extent the neurons are capable
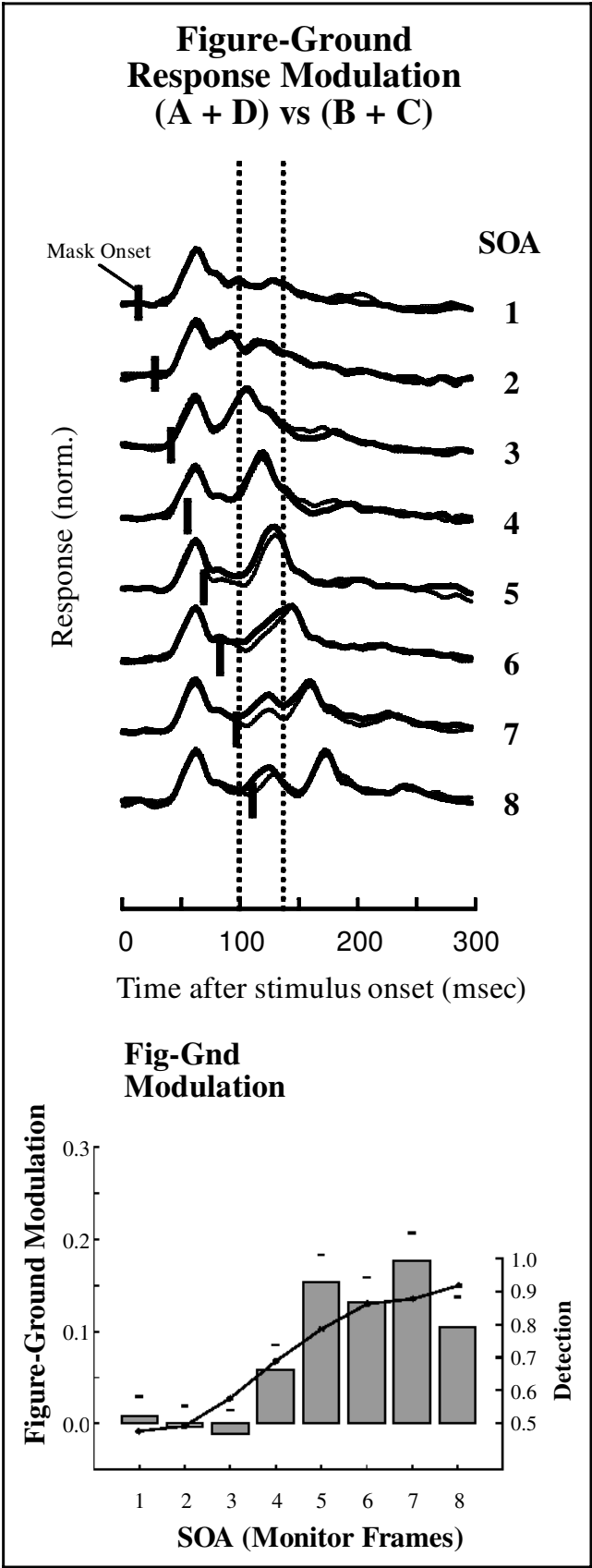
of signalling the difference between the local elements within their RFs (viz Figure 1, left). The most important difference between these elements is, of course, their orientation (45° for A and B, 135° for C and D). However, there are also differences in random organization. The latter influence is somewhat factored out by the fact that for each texture orientation, we had several versions with different random organization (see Methods). For each recording site, we determined which of the two texture orientations was optimally exciting the neurons. We then analyzed to what extent this orientation selectivity is influenced by texture pattern backward masking.

Orientation selectivity at these ''multiunit'' sites is not very strong. For oriented moving bars, the average ratio is 1.94 (see Methods). For the orientation of texture elements, the selectivity is even less pronounced, in part because there were only two orientations, fixed at 45° and 135°, to compare. However, significant differences between optimal and suboptimal texture orientations can be observed at all SOAs except 1 frame (Figure 6 top) (one-sided t test with the electrodes as a group, t statistics for the 1- to 8-frame conditions: 0.38, 1.83, 2.59, 3.37, 2.66, 4.21, 3.56, 4.04, respectively). Orientation selectivity for texture elements arises at much shorter response latency than figure–ground modulation (see also Lamme et al., 1999). Therefore, we quantified the amount of orientation selectivity by taking the mean response levels during a 40-msec interval starting at 50 msec after stimulus onset (dotted line in Figure 6 top). Orientation selectivity for texture elements (Figure 6 bottom) is hardly affected by backward masking (except at an SOA of 1 frame).

As the V1 neurons still signal the difference between the two textures even at very short SOAs, it is conceivable that this information is somehow used (e.g., by higher areas) to segregate figure from ground. According to such a feedforward account of figure–ground segregation, there should be a good match between the neurometric curve of orientation selectivity and the psychometric curve of figure–ground segregation (both obtained during the same experiment with pattern backward masking). In fact, this is not the case. At SOAs where the animals do not perceive the stimuli (2 and 3 frames), orientation selectivity is almost equally strong

Figure 4. Figure–ground responses during pattern masking. Top: Average neural responses (population average of all recorded sites) to the stimulus conditions A and D (see Figure 2), where the RF is covered by figure elements (thick lines), is compared to the average neural response to the stimulus conditions B and C, where the RF is stimulated by background elements (thin lines). This is shown for the eight SOAs. Note the second hump of activity evoked by the mask. Bottom: Difference between figure (A + D) and ground (B + C) responses during the interval shown in the top graphs, for the eight SOAs. Superimposed is the behavioral result from Figure 3.
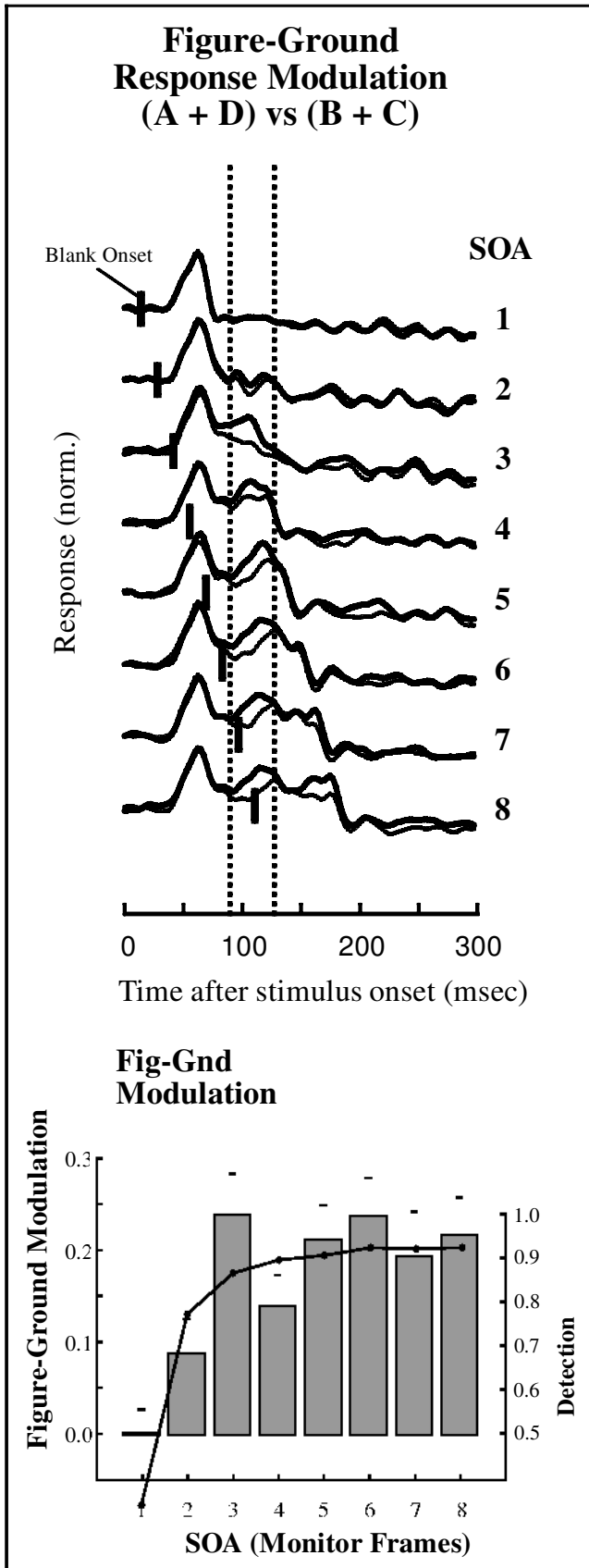
Figure 5. Figure–ground responses during blank masking condition. Legend as in Figure 4, except that the SOAs refer to the interval between figure–ground onset and blank screen onset.

as at SOAs where performance is near perfect. We superimposed neural and behavioral data (Figure 6 bottom, bars vs. line), and using the same method as in the previous section, we found a much worse correspondence (mean squared error = 0.138) than when the same psychometric curve is compared with the neurometric curve of figure–ground modulation (where the error is 0.033, Figure 4 bottom).
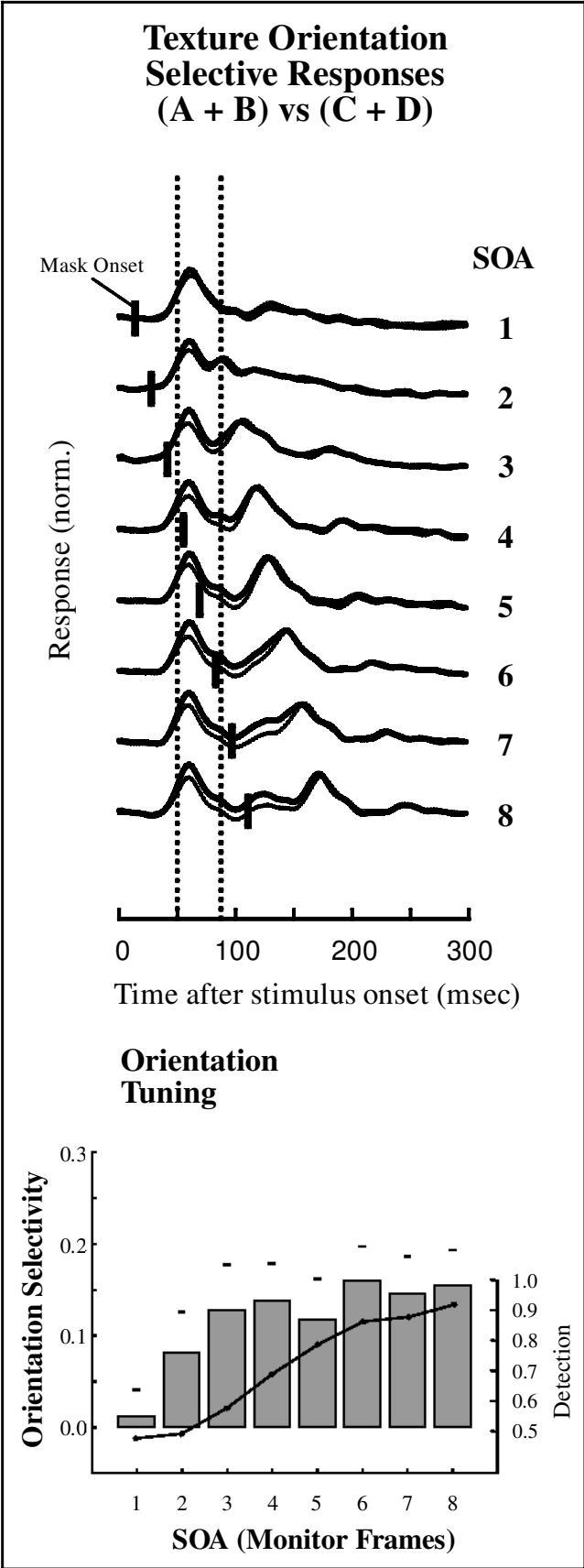
DISCUSSION

We have found that textured figure–ground stimuli can be efficiently masked by a subsequent texture pattern mask (Figure 3 top). V1 neural activity evoked by the figure–ground stimuli is very specifically affected by such backward masking. Contextual modulation, which normally signals the segregation of figure from ground, is selectively suppressed at those stimulus–mask intervals that lead to perceptual invisibility of the figure (Figure 4). Earlier activity, which carries information about the orientation of the elements that make up the figure–ground scene, is not affected by the mask (Figure 6).

This dual finding corroborates our earlier suggestion that within V1, different regimes of activity seem to coexist (Lamme, Supèr, Landman, Roelfsema, & Spekreijse, 2000). There is relatively low-level processing of local features such as orientation, for which V1 is well known, but there is also neural activity related to high-level processes such as figure–ground modulation. The former kind of activity is relatively early, unaffected by masking, and, for example, also remains present when animals are anesthetized (Lamme et al., 1998b) or when animals do not see stimuli (Supèr, Spekreijse, & Lamme, 2001). The latter form of activity occurs at some delay, is affected by masking, is also affected by anesthesia (Lamme et al., 1998b), and is absent when animals report not to see stimuli (Supèr et al., 2001).

Our results show that information about the orientation of the line segments is available in V1 at even the shortest SOAs (2 and 3 frames). If we assume feedforward transfer of information not to be temporally different for the first and second stimulus (i.e., the target and the mask), this information could "safely" reach beyond V1. That this may happen indeed is supported by the finding that backward masking does not affect the early transients of responses in low (Macknik & Livingstone, 1998; Bridgeman, 1980), as well as in high visual areas, including IT (Kovacs et al., 1995; Rolls & Tovee, 1994). It has even been demonstrated by an fMRI and EEG study that information about masked and invisible stimuli can still influence activity up to the motor cortex (Dehaene et al., 1998). It is thus conceivable that the information about the orientation of the line segments is available to the higher cortical areas. Apparently, however, this is not sufficient for the perceptual segregation of figure and background (which is psychophysically near zero

at 2 and 3 frames). Our finding thus supports the view that feedforward processing alone is not sufficient for an organized percept (Lamme et al., 1998a, 1998b; Lamme, 2000; Lamme & Roelfsema, 2000). Only when the stimulus also engages recurrent processing between high and low cortical areas, which results in figure–ground modulation of V1 activity, the animal is able to detect it.

In the prefrontal cortex (the frontal eye field [FEF]), a direct link between the visibility of masked stimuli and late activity has been demonstrated. In these experiments (like in ours), monkeys had to indicate whether masked stimuli were perceived or not by making eye movements towards them. The visual cells of the FEF responded to these masked stimuli, whether perceived or not, with a latency as short as 50 msec. The strongest relation between the neural activity and the monkey's reported percept was observed at latencies of 100 msec and beyond (Thompson, Bichot, & Schall, 1997; Thompson & Schall, 1999, 2000). We analyzed our data to determine whether there was a trial by trial relation between the monkeys report on the visibility of the figure (indicated by the eye movement) and the amount of figure–ground modulation (in the neural data). We did not find any significant effect (data not shown). This confirms our earlier report on the role of figure–ground activity in visual perception (Supèr et al., 2001): There, we found that the presence or absence of modulation determines whether perception will occur. When there is no modulation, there is no perception. However, when there is modulation, this does not in itself guarantee that the animal "reports" to have seen the stimulus. A decision process sits between the modulation and the animals report, which is independent of the modulation. In other words, also in that study, the modulation was not a correlate of the report the animal makes about his percept.

On the basis of the growing data on the neural processing during masking (and on the basis of other evidence, see Lamme, 2000, 2001; Lamme & Roelfsema, 2000), we hypothesize that visual perception goes through several stages: Early on, feedforward processing analyzes the scene in terms of its elementary features. Next, recurrent processing, involving widespread interactions between visual areas including V1 and higher areas, lays the foundations for a coherent percept of the

Texture Orientation Selective Responses (A + B) vs (C + D)

SOA

Mask Onset

Orientation Tuning

Figure 6. Orientation selectivity during pattern masking. Top: Average neural responses (population average of all recorded sites) to the stimulus conditions A and B (see Figure 2), where the RF is covered by optimally oriented line segments (of either figure or ground) (thick lines), is compared to the average neural response to the stimulus conditions C and D, where the RF is stimulated by non-optimally oriented line segments (thin lines). This is shown for the eight SOAs. Bottom: Difference between optimal (A + B) and nonoptimal (C + D) orientations during the interval shown in the top graphs for the eight SOAs. Superimposed is the behavioral result from Figure 3.

scene, where features are combined into objects. When this recurrent activity grows more and more widespread and includes areas in executive space, such as the FEF, a conscious report about this percept (in this case via and eye movement) is possible.

METHODS

Visual Stimulation and Behavioral Control

Stimuli were presented on a 21-in. computer monitor, driven by a No. 9 GxiTC TIGA graphics board. The display resolution was 1024×768 pixels, the refresh rate was 72.4 Hz. The screen subtended $28° \times 21°$ of visual angle. A trial started with the appearance of a $0.2°$ red fixation spot on a texture of randomly oriented line segments. Monkeys were trained to maintain fixation on this spot. Fixation was considered maintained when the eyes did not at any time leave an imaginary $1.0° \times 1.0°$ window centered around the spot. Eye movements were monitored with scleral search coils, according to the modified double magnetic induction method (Bour, Van Gisbergen, Bruijns, & Ottes, 1984). When stored on disk, eye movements were digitized at 400 Hz.

At 300 msec after fixation, the stimulus appeared. This stimulus consisted of a full screen of randomly positioned line segments, either of $45°$ or $135°$ orientation. In a square region of the screen ($3° \times 3°$ wide), the orientation of the line segments was orthogonal to that of the remainder of the screen. This resulted in a textured scene with a square figure overlying a background (see Figure 1 for an impression). The square figure was positioned either to the right or the left of the fixation spot, so that in one of these two positions, the figure covered the RFs of the neurons that we recorded from. In the other figure position, the RFs were covered with background texture. Combining the two texture orientations and the two figure positions resulted in four different stimulus types (A–D, Figure 2). Of each texture of a particular orientation, there were several different versions with different random organization.

The stimuli were presented for variable durations, ranging from 1 monitor frame (14 msec) to 8 monitor frames (110 msec). Subsequently, a mask was presented. This mask was also composed of line segments of either $45°$ or $135°$ orientation. The screen was subdivided in $3° \times 3°$ regions, and these regions were randomly assigned one or the other orientation. Twelve different such masks were used. All trials were blocked in such a way that all four stimulus types (A–D) were equally often followed by any of the 12 mask types. In half of the masks, the RFs were covered with a $45°$ texture, and with a $135°$ texture in the other half. In addition, stimulus and mask textures, even when of the same orientation, used different random positions of the line segments. In a separate set of experiments, the stimuli were not followed by these pattern masks, but simply by a blank screen of approximately equal mean luminance as the textured figure–ground scene. The mask (or the blank screen) remained on until the end of the trial.

At 300 msec after stimulus onset, the fixation spot went off. This was the monkey's cue to make a saccadic eye movement to where he thought the figure was presented (note that at this moment, only the mask or the blank screen was visible). If the eye movement was initiated within 500 msec after the fixation spot went off, and if it landed within the $3° \times 3°$ region of the figure, the trial was considered correct and the animal was rewarded with a drop of apple juice.

Recording of Neuronal Activity

Neural activity was recorded with surgically implanted Trimel-coated platinum–iridium wires 25 μm in diameter, with exposed tips of 50–150 μm. Impedances ranged from 100 to 350 k. , at 1000 Hz. These wires were implanted in the operculum of area 17 (V1) in two macaque monkeys. The obtained signals were amplified ($\times 40,000$), band-pass filtered (750–5000 Hz), full wave rectified, and then low-pass filtered (< 200 Hz). This resulted in a low-frequency signal, representing the "amount" (or envelope) of high-frequency (i.e., spiking) activity (Legatt, Arezzo, & Vaughan, 1980), without any bias for high amplitude spiking neurons, as might be the case when (arbitrary) amplitude thresholds are used to record multiunit activity (MUA). This low-frequency signal was digitized (400 Hz), stored on disk, and analyzed off-line. Aggregate RFs of the neurons contributing to each channel were assessed with moving dark bars over a bright background while the animal was fixating. RF sizes and positions were determined off-line from the responses to these stimuli. Typically, 16 channels, selected from the implanted electrodes on the basis of signal to noise quality of the responses, were recorded simultaneously in each of the two monkeys. For the present experiments, we recorded from 25 of these 32 electrodes in total, selected on the basis of RF position and the presence of contextual modulation. RF eccentricity ranged from $1.3°$ to $5.45°$, and diameter ranged from $0.18°$ to $1.4°$ (mean = $0.52°$). Orientation selectivity was moderately expressed in the MUA. The median orientation selectivity ratio (average response level while a bar of optimal orientation moved over the RF divided by average response for least effective orientation) was 1.94 (mean = 2.19, range = 1.16–9.03). All recording sites could be driven from either of the two eyes. Strong ocular dominance, as has been reported for layer 4C cells (Hubel & Wiesel, 1977), was absent. Given that electrodes were implanted at a range of depths, and given the binocularity of the signals, it is highly unlikely that the moderate

orientation tuning should be regarded as a sign that the recordings expressed mainly layer 4C activity. Instead, taking the RF sizes, tuning ratio and ocular dominance together, we roughly estimate that the electrodes sampled neuronal activity over a distance of some 200–300 μm.

RF positions and sizes stayed stable (within ~0.2°) for many months of recording in these animals. Tuning characteristics could slowly change over periods of weeks or months. The results presented here were collected during weeks of recording in each monkey. For each of the conditions presented (1–8 frames of Texture mask or Blank mask), about 700 trials (total ~11,000) of neural data were collected. The sets of stimuli were presented in randomized or interleaved ways, as to avoid possible electrode drifts to bias the results.

Data Analysis

To calculate poststimulus time responses, 300-msec epochs following stimulus onset were averaged from those trials where the animal had at least fixated until the fixation spot went off. The mean of the signal obtained at 0–30 msec after stimulus presentation was subtracted from the signal. For all practical purposes, this can be considered the amount of activity that was present while the animal fixated the prestimulus texture (Lamme, 1995; Lamme et al., 1998b). Some sites exhibited activity that was locked to the monitor framerate (72.4 Hz). Therefore a digital 72.4-Hz notch filter was applied. The displayed responses were additionally smoothed with 1–2–1 windows.

At different electrodes, responses were obtained, which differed strongly in their magnitude. Suppose that at one electrode, the responses that are obtained are twice as big as at another electrode. With normal response averaging, the response of the first electrode would have twice the effect on the average as the second. We wanted all electrodes to have an equal contribution to the population average. Therefore, we normalized at each electrode all responses obtained for all stimulus conditions to the maximum response obtained at that electrode. In this way, all electrodes contributed equally, but relative response differences between conditions (e.g., figure vs. ground or the different SOAs) at each electrode remained unaltered.

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