J Neurophysiol 94: 4331–4343, 2005.
First published August 17, 2005; doi:10.1152/jn.01312.2004.

Background Changes Delay the Perceptual Availability of Form Information

Xin Huang, Seth Blau, and Michael A. Paradiso

Department of Neuroscience and Brain Science Program, Brown University, Providence, Rhode Island

Submitted 20 December 2004; accepted in final form 14 August 2005

Huang, Xin, Seth Blau, and Michael A. Paradiso. Background changes delay the perceptual availability of form information. *J Neurophysiol* 94: 4331–4343, 2005. First published August 17, 2005; doi:10.1152/jn.01312.2004. In natural visual situations, unlike most psychophysical experiments, when a new stimulus appears in a portion of the visual field, the surrounding background changes simultaneously. In recordings from macaque V1, we found that a visual stimulus presented simultaneously with a background change evokes a response that is qualitatively different from the response to the same stimulus flashed on a static background. With the changing background, information about stimulus orientation and contrast is significantly delayed compared with the static-background situation. Our physiological results make several predictions that we test in the present paper with human psychophysical experiments. In a backward masking paradigm, a bar stimulus was either flashed onto a static background or presented simultaneously with a change in background luminance or pattern. Subjects discriminated bar orientation or detected that the scene changed before the mask. To achieve an equivalent contrast threshold for orientation discrimination, a longer stimulus-mask onset asynchrony (SOA) was needed in the changing than in the static-background condition; to match the orientation discrimination performance in the static and changing-background conditions at a fixed SOA, a higher bar contrast was needed when the background changed. Moreover, in the changing-background condition, a longer SOA was needed to discriminate bar orientation than to detect the scene change. These results suggest that orientation information is available more slowly when the background changes; orientation information is available earlier as stimulus contrast increases. The psychophysical findings are consistent with our physiological predictions. Compared with the common technique of flashing stimuli onto a static background, the changing-background paradigm may be more similar to natural vision in which saccades bring new stimuli and backgrounds into the visual field.

INTRODUCTION

Most physiological and psychophysical experiments exploring visual perception use a simple paradigm in which the subject fixates and stimuli are flashed into a portion of the visual field. While this procedure provides great control over visual stimulation, it is unnatural in two regards. First, in natural visual situations, stimuli are usually brought into a portion of the visual field as a consequence of saccadic eye movements—they do not suddenly flash into view. Second, as a consequence of eye movements, when one stimulus is brought into a portion of the visual field, there are concurrent changes in the background. The assumption implicit in most experiments is that in natural situations visual performance would be comparable to that recorded in the reduced laboratory paradigm. In this study, we measured detection and discrimination thresholds over time to examine the validity of this assumption.

The psychophysical experiments reported here were motivated by the results of neural recordings in primary visual cortex (V1) of macaque monkeys (Huang and Paradiso 2005). The physiological experiments were a first step moving toward more natural visual stimulation, while preserving a considerable degree of stimulus control. Although a stimulus was still flashed into the receptive field (RF) of a fixating animal, this stimulus was introduced along with a background change in either luminance or texture (simulating the background change that would result from a saccade). We found that the temporal response patterns of macaque V1 neurons depend strongly on the manner in which stimuli are introduced into RFs. When a "local" stimulus was introduced into the RF of a macaque V1 neuron along with a change in the background, the responses were qualitatively different from those observed with a static background. When a stimulus in the RF was presented concurrently with a background change, the representation of stimulus contrast and orientation was delayed. Some of the V1 neurons showed a biphasic response, comprised of a rapid rise to peak activity, a fall from this peak, and a relatively long delayed-response plateau (Fig. 1*B*); others showed only the delayed response component (Fig. 1*C*). Stimulus contrast was found to be anti-correlated with the latency of the delayed response (Fig. 1, *E* and *F*), and orientation was found to be reflected in the magnitude of the delayed response (Fig. 1, *B* and *C*). Compared with the delayed response, the early transient portion of the response was less sensitive to stimulus contrast and orientation. Instead of conveying form information about the local stimulus, the early response appeared to signal that the scene had changed (Fig. 1, *B* and *D*). The response pattern observed with a changing background is in contrast to that found when a local stimulus was flashed on a static background (Fig. 1*A*). In this latter situation, orientation, and contrast were reflected in the early neural response.

The different response patterns observed with stimuli flashed on a static background and a changing background (hypothesized to be the more natural situation) lead to several predictions for visual perception (see Fig. 1): *1*) with a background change, the availability of feature information should be delayed relative to the case with a static background; *2*) the ability to discriminate the form of a visual stimulus presented with a background change should be delayed relative to the ability to detect the change of the visual scene; and *3*) increasing the contrast of a stimulus should speed the availability of feature information.

Address for reprint requests and other correspondence: M. A. Paradiso, Dept. of Neuroscience, 192 Thayer St., Brown University, Providence, RI 02912 (E-mail: Michael_Paradiso@Brown.edu).

The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked "*advertisement*" in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

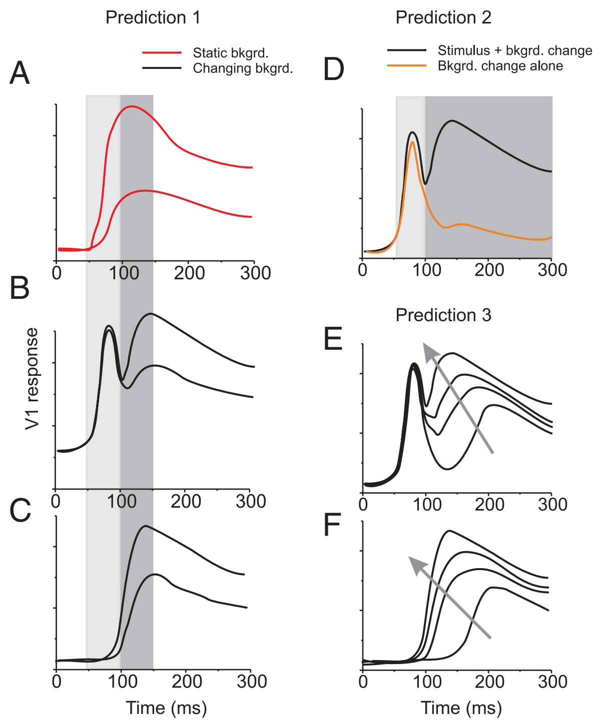

FIG. 1. Schematic physiological results and psychophysical predictions. *A–C*: schematic V1 responses to 2 different stimulus orientations. In the static-background condition (*A*), the responses diverge early (vertical light gray shading). With a background change, the responses diverge at a later time (vertical dark gray shading) for neurons showing biphasic (*B*) and delayed-only responses (*C*). These physiological results lead to *prediction 1,* which is that with a background change, the availability of orientation information should be later than with a static background. *D*: in the changing-background condition, orientation information is found in the delayed response (dark gray shading) rather than the early response transient (light gray shading). The early transient response appears to register a visual scene change (as in the background change alone condition). *Prediction 2* is that the ability to discriminate the form of a visual stimulus presented with a background change should be delayed relative to the ability to detect the change of the visual scene. *E* and *F*: schematic V1 responses to various stimulus contrasts in the changing-background condition. As stimulus contrast increases, the latency of the delayed response from the neurons showing the biphasic response profile (*E*) and the response latency of the neurons showing the delayed-only response (*F*) decrease (arrow pointing the direction of contrast increment). *Prediction 3* is that increasing the contrast of a stimulus should speed the availability of orientation information.

We tested these predictions in detection and discrimination experiments with human observers. The general approach was to use backward masking to attempt to interfere with responses in visual cortex. Placed at particular time delays after stimulus onset, a mask may interfere with the delayed response more than the early response. Because information about stimulus form is available in the early response with a static background and is carried more in the delayed response with a changing background, a delayed mask might disrupt form discrimination with a changing background more than with a static background. Following similar logic, if detecting a scene change is based on the relatively unselective initial response in the changing-background condition and discriminating stimulus features is more dependent on the delayed response, discrimination performance may be impaired more than detection when masking interferes with the delayed component. Some results of this study have been published previously in abstract form (Huang et al. 2001).

METHODS

Visual stimuli

Stimuli were displayed on a 19-in monitor (640 × 480 pixel resolution) with a refresh rate of 163 Hz. An oriented bar 1.7 × 0.3° in size was presented at the fixation point either on a uniform gray background or on a textured background. The textured background was composed of random dots with two gray levels at 0.02 and 19.2 cd/m^2. The texture background was randomized at the single-pixel scale (each pixel subtended 0.06°). In this way, mean luminance was preserved at as fine a spatial scale as possible when the background changed. The mean luminance of both the uniform gray background and the textured background was 9.6 cd/m^2. When no stimulus was displayed (a "black" screen) the luminance was 0.02 cd/m^2. The visual display was controlled by MatVis software (Neurometrics) running under Matlab (Mathworks).

Three types of visual masks were used in the experiments. One was a uniform light mask, with a luminance of 66.5 cd/m^2. The second was a combination of light and pattern mask (Fig. 2*A*). The mask pattern was composed of superimposed bars covering all possible orientations that the stimulus bar might take. The size of the mask bars was the same as that of the stimulus bar. The masking bars had a luminance of 68.0 cd/m^2, and the gray area around them had a luminance of 40.8 cd/m^2. In the experiments using textured pattern backgrounds, a third mask was used combining the superimposed oriented bars and a two-gray-level random dot background (Fig. 2*B*). The mask had a background dot pattern identical to the background of the stimulus except that the pixels at 0.02 and 19.2 cd/m^2 in the stimulus background were replaced with pixels of 28.8 and 67.2 cd/m^2 in the mask, respectively.

Procedure

One naïve subject and two of the authors, all with normal or corrected-to-normal vision, participated in the experiments. Unless specified otherwise, all experiments used the following procedure (Fig. 2). Subjects sat at a distance of 57 cm from the visual display. In the static-background condition, a central fixation point was shown on a uniform gray background or a textured background for 920 ms. Subjects fixated and a stimulus bar was flashed at the fixation point for two video frames (12 ms) after which the bar and background were extinguished. In the changing-background condition, the fixation point appeared first on a black screen or a textured background for 920 ms. A stimulus bar was then presented simultaneously with a change in the background (either black to uniform gray or one texture pattern to a different pattern). In both the static and the changing-background conditions, the visual display returned to uniform black 12 ms after the stimulus bar was turned on. After a variable time delay, a mask was presented for 307 ms after which the screen was returned to black for an inter-trial interval lasting 1,840 ms. *The key point is that discriminations made in the static and changing-background conditions used identical stimuli; the only difference in the paradigms was the background preceding the discrimination target.* As described in the following text, subjects performed a temporal two-alternative-forced-choice (2AFC) task.

In some experiments, a staircase method was used to track the contrast threshold for orientation discrimination or detection (79% correct performance). The luminance of the oriented bar was changed adaptively with a variable step size, cut in half after each reversal. Threshold was defined as the average of the last six reversals of the staircase. Every data point in the figures represents the mean of three separate threshold measurements. In other experiments, the method of constant stimuli was used to construct psychometric functions. Subjects ran three blocks of 30 trials each and the data points were fit with sigmoidal (Boltzmann a.k.a. logistic) functions using Origin (Origin-

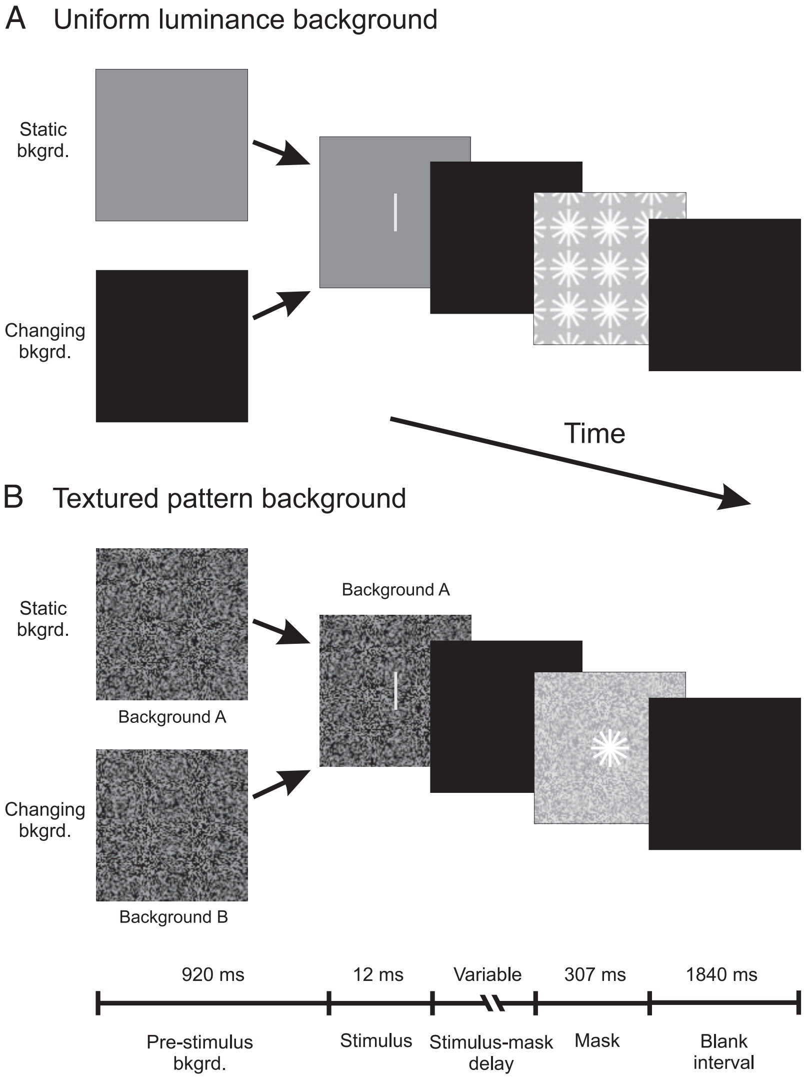

FIG. 2. Experimental procedure and timing. A bar stimulus was presented on a background with either uniform luminance (*A*) or a random texture pattern (*B*). *A*: in the static-background condition, the bar was presented on a gray background. In the changing-background condition, the background changed from black to gray when the bar was introduced. *B*: the bar was presented on a texture pattern that was either identical (static background) or different (changing background) from the background present before the bar. Textured pattern backgrounds *A* and *B* had the same mean luminance. As illustrated, different masking stimuli were used in the uniform luminance and texture pattern experiments. Stimulus-mask onset asynchrony (SOA) was controlled by varying the stimulus-mask delay. In the experiments using a temporal 2AFC procedure, 2 sequential sequences, as illustrated here, were presented.

Lab). The mathematical function for sigmoidal fitting was: $y = B + \dfrac{A - B}{1 + e^{(x - x_0)/W}}$, where A and B are upper and lower plateau values, x_0 is the value of x at which $y = \dfrac{A + B}{2}$, and W is the width variable. The curve fit minimized χ^2 (i.e., the summed square error divided by the number of degrees of freedom).

RESULTS

Experiment 1: orientation discrimination with or without a change in background luminance

When a new "local" stimulus is brought into a portion of the visual field by a saccade, the background luminance level often changes (Huang and Paradiso 2005). Here we explore the consequence of the background change for orientation discrimination performance. This experiment also tests the prediction, based on our physiological recordings, that with a luminance change in the background the availability of feature information is delayed relative to the situation with a static background.

A. VARYING STIMULUS-MASK ONSET ASYNCHRONY (SOA). *Method.* The staircase technique was used to measure the threshold bar luminance needed to achieve 79% correct performance on an orientation discrimination task. Subjects were required to select which of two successive intervals contained a bar that was tilted more counter-clockwise. The orientation difference of the stimulus bars was 30°. In both static- and changing-background conditions, discriminations were made with identical bars on identical gray backgrounds. In the static-background case, the bar was simply flashed onto a static gray background; in the changing-background condition, the bar and gray background were presented simultaneously from a preceding display that was black. A combined light and pattern mask was used in this experiment.

We also used the method of constant stimuli to construct psychometric functions to characterize the temporal properties of orientation discrimination. The discrimination task was otherwise identical to that described in the preceding text. A fixed bar luminance was chosen for each subject based on his performance in the experiment using the staircase procedure (*SB*: 12.8 cd/m^2, *TH*: 14.3 cd/m^2, *XH*: 13.8 cd/m^2).

Results. As SOA increases, the threshold bar luminance for orientation discrimination decreases (Fig. 3*A*). This is consis-

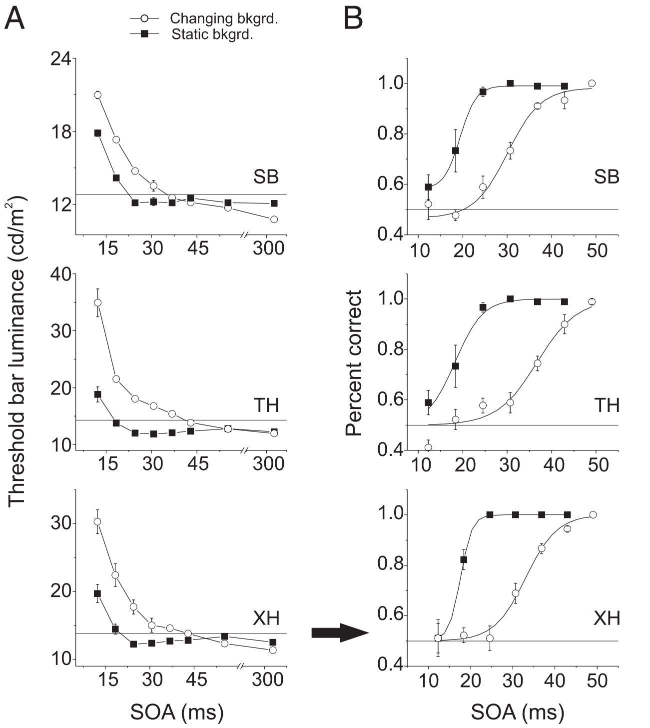

FIG. 3. Orientation discrimination with or without a background luminance change. *A*: threshold bar luminance measured with a staircase procedure. At shorter SOAs, thresholds are higher in the changing-background condition. To achieve the same threshold level, a longer SOA is needed in the changing-background condition. *B*: orientation discrimination performance measured with the method of constant stimuli at a fixed bar luminance (horizontal lines in *A* indicate bar luminances used for *B*: *SB,* 12.8 cd/m^2; *TH,* 14.3 cd/m^2; *XH,* 13.8 cd/m^2). Curves in *B* are sigmoidal fits to the data points. —, chance performance. Longer SOAs are needed to achieve the same level of performance with the changing background. ○, changing-background condition; ■, static-background condition. The background luminance was either kept at 9.6 cd/m^2 (the static background) or was changed from 0.02 to 9.6 cd/m^2 (the changing background).

tent with type A masking reported in previous backward masking studies (see Breitmeyer 1984 for review). At SOAs longer than ~50 ms, performance in the static- and changing-background conditions is similar for all observers, suggesting that task difficulty in the two conditions is comparable. Interestingly, to achieve the same luminance threshold in the intermediate range, a longer SOA is needed in the changing-background condition than in the static-background condition. Across subjects, the SOA difference required to match the luminance thresholds ranged from 5 ms (Fig. 3*A, top,* at threshold ~18 cd/m^2) to 34 ms (*middle* at threshold ~13 cd/m^2) as bar luminance decreased (before reaching asymptote). At any SOA shorter than ~40 ms, the luminance threshold is higher in the changing-background condition than in the static-background condition. The difference is large at the shortest SOAs and becomes smaller as SOA increases. This suggests that, at shorter SOAs, the mask interferes more with orientation discrimination in the changing-background condition than in the static-background condition. These results were obtained with a light and pattern mask, but qualitatively similar results were found with a uniform light mask.

Figure 3*B* shows orientation discrimination performance at different SOAs measured with the method of constant stimuli when the bar luminance was fixed. To achieve the same performance level, a longer SOA is needed in the changing-background condition than in the static-background condition. Based on the fitted sigmoidal functions, at the 79% correct level, the SOA differences between the static- and the changing-background conditions are 13 ms (*SB*), 19 ms (*TH*), and 16 ms (*XH*) respectively. At a SOA of ~25 ms, the performance of all three subjects is nearly perfect in the static-background condition but near chance when there is a background luminance change.

These findings are consistent with the physiological data in that orientation information appears to be represented at a distinctly earlier time when the stimulus is presented on a static background than when the stimulus is introduced simultaneously with a background luminance change. Moreover, stimulus contrast has a similar effect in the psychophysical and neural data. In orientation discrimination, the difference in SOA needed to match performance in the static- and changing-background conditions increases as bar luminance decreases (Fig. 3*A*). This is consistent with the increase in neural latency difference, as stimulus contrast decreases, between the early response carrying orientation information in the static-background condition and the delayed response carrying orientation information in the changing-background condition.

B. VARYING STIMULUS ONSET. *Method.* Orientation discrimination performance was quantified at different stimulus contrasts with the method of constant stimuli. In this experiment, there was only one stimulus interval rather than the two-interval 2AFC used in the preceding text. On each trial either a horizontal or a vertical bar was presented for 12 ms with or without a background luminance change. A uniform light mask was introduced at a fixed SOA of 18 ms. Subjects were required to report the bar orientation (2AFC) after each trial. Different bar contrasts and the conditions with and without the background luminance change were randomly interleaved. The visual display went black in the inter-trial interval and in the changing-background condition the background returned to gray when the bar stimulus was presented. In the static-background condition, the gray background was introduced 2,760 ms before the stimulus bar. Stimulus bar contrast was calculated by the formula: $\frac{\mathrm{Lum}_{\mathrm{Bar}} - \mathrm{Lum}_{\mathrm{Backgrd}}}{\mathrm{Lum}_{\mathrm{Bar}} + \mathrm{Lum}_{\mathrm{Backgrd}}}$, where Lum_{Bar} is the luminance of the stimulus bar, $Lum_{Backgrd}$ is the mean luminance of the background.

Results. Figure 4 shows that performance improves as bar contrast increases in both the static- and changing-background conditions. To achieve the same percent correct on the discrimination, significantly more bar contrast is required in the changing-background condition. At many contrast levels, there were dramatic differences in performance. For example, at bar contrasts of 0.16 for *TH* and *XH* and 0.23 for *SB,* subjects could discriminate bar orientation very well with a static background, but they performed near chance with the changing background. These results are consistent with the delayed representation of orientation information found in the physiological experiments and the effect of contrast. As contrast is increased, orientation information appears to be available more quickly in the changing-background condition, but it is always slower than in the static-background condition.

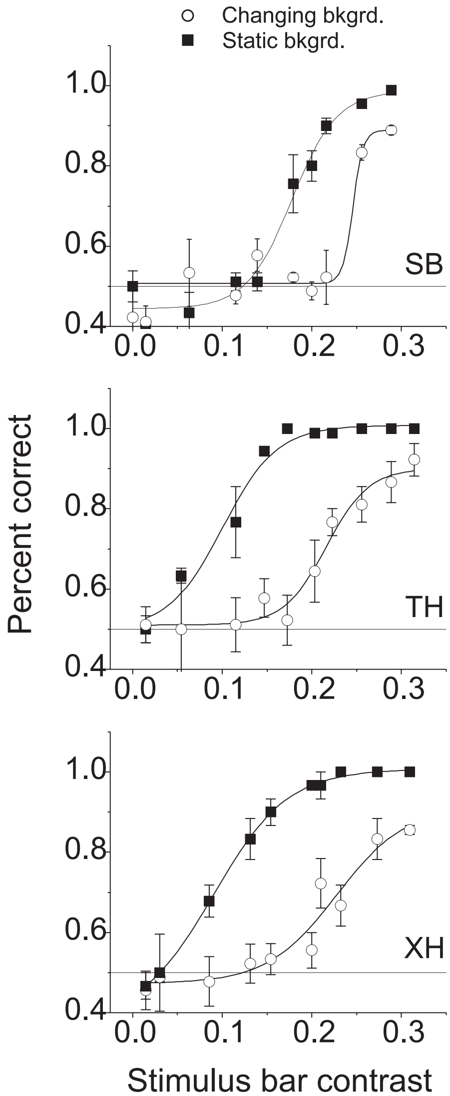

FIG. 4. Effect of stimulus contrast on orientation discrimination. At a fixed SOA (18 ms), performance improves as contrast increases. Higher contrasts are needed to achieve the same level of performance in the changing background. ○, the changing-background condition; ■, the static-background condition. Curves are sigmoidal fits to the data points. —, chance performance.

C. VARYING BACKGROUND VERSUS STIMULUS BAR ONSET ASYNCHRONY. In the experiments described in the preceding text, we showed that the threshold for orientation discrimination in the changing-background condition was higher than in the static-background condition. Of course, in the static-background condition, the gray background was not *always* present; it was simply introduced well before (920 or 2,760 ms) presentation of the stimulus bar. So how long must the gray background be present before the stimulus bar to yield “static” background data? To answer this question, we varied the time between background onset and stimulus bar onset. In doing so, we were able to follow the development of the static/changing-background threshold difference.

Method. The staircase technique was used to measure the threshold bar contrast needed to achieve 79% correct performance on an orientation discrimination task. On each trial, there was a single stimulus interval during which either a horizontal or a vertical bar was presented for 12 ms, followed by a mask of uniform light at a SOA of 18 ms. Subjects were required (2AFC) to report the bar orientation. In the inter-trial interval, the visual display was black. A gray background (9.6 cd/m^2) was introduced between 0 and 2,760 ms before the onset of the stimulus bar. If the background/bar onset asynchrony was zero, the situation was equivalent to the changing-background condition used in earlier experiments. If the onset asynchrony was 2,760 ms, the situation was equivalent to the static-background condition in *experiment 1B*. Subjects *SB* and *XH* participated in the experiment.

Results. The data for bar threshold at different background/bar onset asynchronies are shown in Fig. 5. To allow a comparison with the results already presented, reference horizontal lines are plotted for the static- (• • •) and changing-background (—) data from *experiment 1B*. The contrast threshold for orientation discrimination is highest when the background comes on before the bar by a time between 0 and 50 ms. By ~50 ms, the threshold has fallen back to the level observed with the changing background (i.e., threshold at 0 ms). As the background/bar onset asynchrony increases beyond 50 ms, the threshold falls, ultimately reaching at about 250 ms the static background threshold. In other words, it appears that if the gray background is present 250 ms before the bar is introduced, perception of the bar is comparable to the situation in which the background had been gray for a much longer time.

The initial increase of the contrast threshold between 0 and 50 ms is likely to be a result of forward masking that occurs

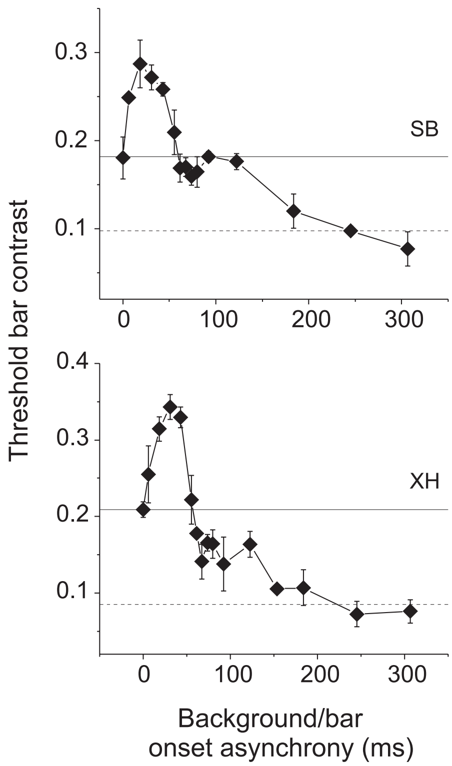

FIG. 5. Dependence of contrast threshold for orientation discrimination on background/bar SOA. An asynchrony of 0 ms corresponds to the changing-background condition in *experiment 1B* (—) and an asynchrony of 2,760 ms corresponds to the static-background condition (- - -). Stimulus-mask onset asynchrony was fixed at 18 ms. At very short SOAs, threshold is elevated, probably from forward masking. If the background appears more than ~250 ms prior to the bar, data are similar to the static-background situation.

when the gray background and bar are turned on in rapid succession. The fall of the threshold to the static-background level by 250 ms is important as it indicates that prolonged adaptation to the gray background is not necessary to see the effects that we have observed. The background/bar onset asynchrony required to obtain static-background results is comparable to 200–300-ms duration of typical fixations. Our results suggest that the ability to discriminate an isolated stimulus introduced into the visual field at the end of a fixation period is different from the ability to discriminate the stimulus when it is introduced simultaneously with a background change. Stated another way, the thresholds measured in typical psychophysical experiments in which fixation is prolonged before a stimulus is presented (a static condition) are probably significantly lower than those in natural vision (in which the background changes with each shift in fixation).

Experiment 2: comparison of detection and discrimination with or without a background luminance change

An implication of our V1 recordings is that early and late action potentials convey qualitatively quite different information in the changing-background condition. While the initial response was comparable in latency to that observed with a static background, the early response in the changing-background condition appeared to signal only that the scene had changed; it was relatively unselective for stimulus orientation and contrast. Many V1 neurons also showed a comparable initial response to the background change even if no bar was present. Based on these observations, we predicted that in the changing-background condition the early response would provide human observers with information only about whether the scene had changed (i.e., that something in the background or bar was different even though the specifics of the change might not be discriminated). Because the delayed response carried information about orientation (and contrast), we predicted that human orientation discrimination should be delayed relative to the ability to detect that the scene had changed. To test these predictions, we examined the temporal aspects of detection and orientation discrimination in the static- and changing-background conditions. As described in detail in the following text, detection and discrimination were measured with identical stimuli.

Method. The staircase method was used to measure the threshold bar luminance required for detection with a two-interval 2AFC task. As in *experiment 1A,* a combination light and pattern mask was presented at various SOAs. In the static-background condition, one of two successive stimulus sequences contained a bar, and in the other sequence, the display remained at the same luminance level with no bar introduced. The task was to choose which sequence contained a bar. In the background luminance change condition, one of two stimulus sequences contained a visual scene change (introduction of a bar plus change of background luminance) and in the other sequence the display remained black. The subjects' task was to report which of the two successive intervals contained a visual scene change based on either the bar or background.

Performance was also measured at various SOAs with the method of constant stimuli. A fixed bar luminance was selected for each subject (*SB*: 12.8 cd/m^2, *TH*: 14.3 cd/m^2, *XH*: 13.8 cd/m^2) and was used in the detection task described in the preceding text.

Results. Figure 6*A* shows the threshold bar luminance required to detect a scene change at different SOAs in the changing-background condition. For comparison, the figure also replots the threshold bar luminance required for orientation discrimination in the changing-background condition measured in *experiment 1A.* As SOA increases, the threshold bar luminance for both orientation discrimination and scene change detection decreases. To achieve the same threshold level, a longer SOA is needed for orientation discrimination than for scene change detection.

In the scene-change detection paradigm, the threshold reaches its asymptotic level at a SOA of approximately 20–30 ms. For all three observers, the asymptotic bar luminance was 9.6 cd/m^2, which is the same as the luminance of the gray background (i.e., the bar was no longer visible). In other words, at SOAs longer than ~30 ms, subjects could detect the visual scene change based simply on the background luminance change. At shorter SOAs the presence of a more luminous bar on the background was needed to detect that the scene had changed. At the longest SOA (319 ms) tested, the threshold bar luminance for orientation discrimination is slightly higher than that for scene change detection. Of course this must be the

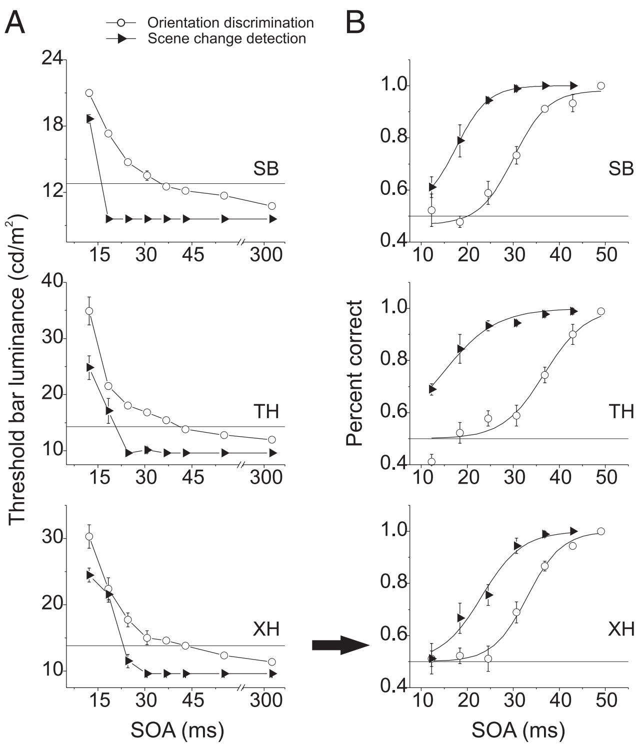

FIG. 6. Comparison of scene change detection and orientation discrimination with a background luminance change. *A*: threshold bar luminance for orientation discrimination and scene change detection at different SOAs. Performance improves as SOA increases, reaching asymptotic values at shorter SOAs for detection. *B*: orientation discrimination performance at a fixed bar luminance (— in *A* indicate bar luminances used for *B*: *SB,* 12.8 cd/m^2; *TH,* 14.3 cd/m^2; *XH,* 13.8 cd/m^2). Performance in both detection and discrimination improves as SOA is increased, but detection rates saturate at significantly shorter SOAs. Curves in *B* are sigmoidal fits to the data points. —, chance performance. ○, orientation discrimination; ▲, scene change detection.

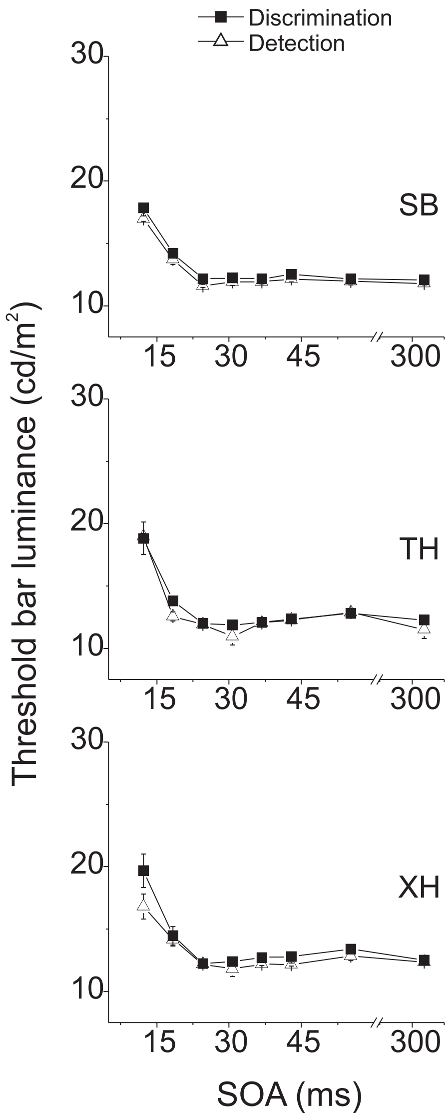

FIG. 7. Comparison of scene change detection and orientation discrimination in the static-background condition. Threshold bar luminance for discriminating the bar orientation (■) and for detecting the presence of the bar (△) are similar at all SOAs.

case as orientation discrimination requires that the bar luminance be above that of the background.

Figure 6*B* compares detection and discrimination performance at different SOAs when the bar contrast is fixed. To achieve the same performance level, a longer SOA is needed for orientation discrimination than for scene change detection. The SOA difference between discrimination and detection at the 79% correct level is 14 ms (*SB*), 22 ms (*TH*), and 10 ms (*XH*), respectively. Comparison of the data "vertically" highlights the critical influence of timing for the two tasks. For example, at a SOA of ~25 ms, subjects are nearly perfect on detection but near chance on discrimination.

Data collected in the static-background condition suggest that the availability of information for detection and discrimination is strikingly different from the changing-background condition. Threshold bar luminance in the static-background condition is shown in Fig. 7. The thresholds for orientation discrimination and detection are virtually identical at all SOAs.

These results are consistent with our physiological finding that with a changing background, form information is delayed relative to information signaling that the scene has changed (presumably resulting from a saccade in natural situations). In the static-background condition, a large detection/discrimination difference is not observed in the psychophysical or physiological data.

Experiment 3: detection and discrimination with or without a background pattern change

In natural viewing conditions, saccades produce changes in both the luminance and pattern at any given location in the visual field (see DISCUSSION of previous paper). *Experiments 1* and *2* examined detection and discrimination with a background luminance change but no pattern change. Here we describe complementary experiments in which the background pattern changed, but the luminance was constant. As illustrated in Fig. 2*B,* in the static-background condition, an isolated bar was flashed onto a textured background pattern A; in the changing-background condition, textured background B was displayed first and a stimulus bar was presented simultaneously with a change from background B to background A.

A. ORIENTATION DISCRIMINATION WITH OR WITHOUT A BACKGROUND PATTERN CHANGE. *Method.* The experimental procedure was the same as in *experiment 1A,* using both staircase and method of constant stimuli procedures. The background stimuli were texture patterns with fixed mean luminance as described in METHODS. The masking stimulus was a combined noise and pattern mask.

Results. The data in Fig. 8*A* show that to achieve the same threshold level, a longer SOA is needed when the background pattern changes than when it is static. At the same SOA, threshold bar luminance is higher with a changing- than a static-pattern background. However, it is important to note that even at the largest SOAs the conditions yield quite different asymptotic threshold levels. This suggests that the tasks differ significantly in difficulty and cannot be simply compared in this way. Data in Fig. 8*B* were obtained with a fixed bar luminance (16.8 cd/m^2 for *SB,* 14.6 cd/m^2 for *TH,* 15.1 cd/m^2 for *XH*). To achieve the same performance level, a longer SOA is needed in the changing-background condition than in the static-background condition. However, the slope of the curve for the static-background data is significantly steeper than for the changing-background data, suggesting that the static task is fundamentally easier.

B. ORIENTATION DISCRIMINATION ADJUSTED FOR TASK DIFFICULTY. In this experiment, we attempt to equate task difficulty and reexamine orientation discrimination with or without a background pattern change. *Subjects SB* and *XH* participated in the experiment. The same staircase method that was employed in *experiment 3A* was used. We first repeated the orientation discrimination experiment but without a mask. The presentation duration of the stimulus bar was varied to determine a duration at which the bar luminance thresholds in the static- and changing-background conditions are the same. This was achieved with stimulus durations >31 ms (Fig. 9*A*). We then repeated the backward masking experiment using a bar duration of 37 ms.

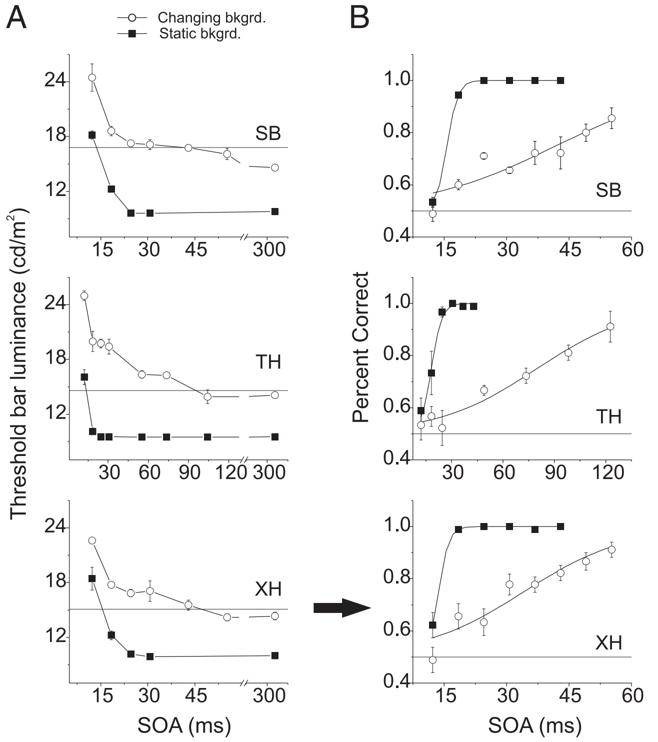

FIG. 8. Orientation discrimination with or without a background pattern change. *A*: threshold bar luminance for orientation discrimination at different SOAs. Threshold is higher with a changing background, but the difference in performance at long SOAs suggests that the task is fundamentally more difficult with the changing background. *B*: orientation-discrimination performance at a fixed bar luminance (— in *A* indicate bar luminances used for *B*: *SB,* 16.8 cd/m^2; *TH,* 14.6 cd/m^2; *XH,* 15.1 cd/m^2). Curves in *B* are sigmoidal fits to the data points. —, chance performance. ○, background pattern change; ■, static-background pattern. Note the SOA scale for *subject TH* is different from the other subjects' scale.

Results. Figure 9*B* shows threshold bar luminance for orientation discrimination (with a mask) with the 37-ms bar duration. Because of the longer stimulus duration, performance in the static-background condition is at its asymptotic value even at the shortest SOAs. In other words, there is no effect of reintroducing the mask. However, the mask has a significant effect on performance with the changing background. At the shortest SOAs, the threshold luminance nearly doubled when the mask was used. A significantly longer SOA is needed in the changing-background condition (~80–90 ms) for the threshold to reach the level found in the static-background condition with an SOA of 37 ms. Thus after correcting for task difficulty, it appears that form information is delayed in the changing-background condition when a changing-background pattern is used and background luminance is held constant.

C. COMPARISON OF ORIENTATION DISCRIMINATION AND SCENE-CHANGE DETECTION WITH A BACKGROUND PATTERN CHANGE. *Method.* To compare the timing of detection and discrimination with a background pattern change (with no luminance change), we collected detection data using the staircase procedure. A combined noise and pattern mask was used. One of two stimulus sequences contained a visual scene change (introduction of a bar plus change of background pattern), and in the other sequence, the display stayed at a fixed background pattern. The subject reported which sequence contained a scene change.

Results. When detection thresholds were collected with the procedure described in the preceding text we found that to reach comparable performance levels, significantly longer SOAs were required for orientation discrimination than scene change detection. However, as in *experiment 3A,* it was clear that the discrimination task was fundamentally more difficult than the detection task. We therefore used the procedure described in *experiment 3B* to equate task difficulty in the discrimination and detection tasks. We found that with no mask and a stimulus duration of 37 ms, the threshold bar luminance for scene change detection equaled the threshold for orientation discrimination (Fig. 10*A*). This longer duration was then used in new experiments with the mask reintroduced.

With a stimulus duration of 37 ms, performance on the detection task is at its asymptotic value at the shortest SOA; there is no improvement as SOA increases and reintroducing the mask has no effect on threshold (Fig. 10*B*). However, adding the masking stimulus significantly impaired performance on orientation discrimination, nearly doubling luminance thresholds at the shortest SOA. To obtain comparable luminance thresholds for discrimination and detection, a SOA of approximately 80–90 ms is required, consistent with the hypothesis that information useful for detecting that something has changed is present earlier than information about stimulus form (needed for orientation discrimination).

DISCUSSION

Our findings concerning the temporal properties of detection and discrimination have important implications for the interpretation of previous psychophysical experiments as well as vision in more natural situations. The data also have compelling parallels with form selectivity in visual cortical activity and suggest a connection between V1 activity and temporal aspects of detection and discrimination.

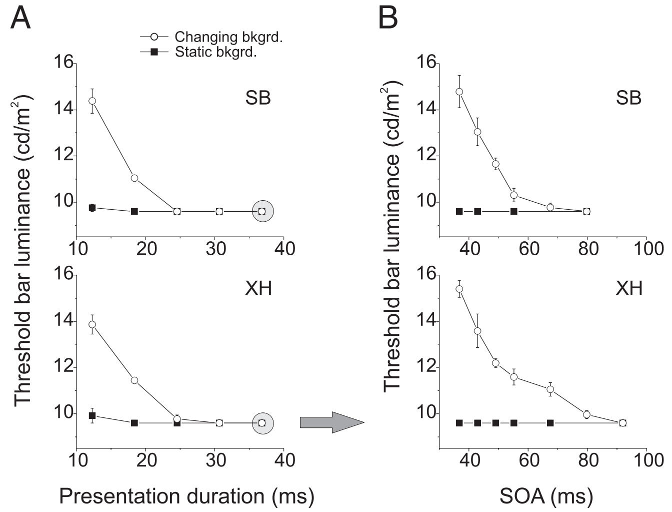

FIG. 9. Equating task difficulty for orientation discrimination with or without a background pattern change. *A*: without a masking stimulus, threshold bar luminances in the static- and changing-pattern background conditions are equivalent with stimulus durations >31 ms. *B*: using a stimulus duration of 37 ms, the masking stimulus was reintroduced and thresholds measured across SOA. The mask raises the threshold significantly with the changing background but not with the static background. A SOA of ~80–90 ms is required for the changing-background threshold to fall to the level of the static-background threshold. ○, background pattern change; ■, static-background pattern.

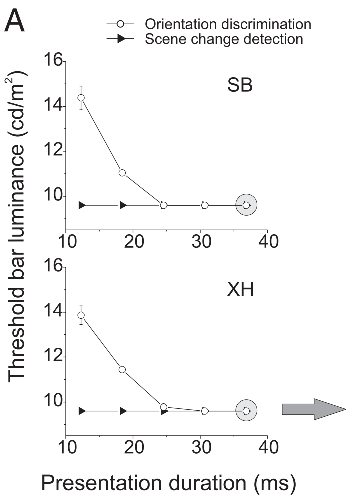

FIG. 10. Equating task difficulty for orientation discrimination and scene-change detection in the background-pattern-change condition. *A*: thresholds for detection and discrimination were equivalent with stimulus durations >31 ms when no masking stimulus was used. *B*: using a stimulus duration of 37 ms, the masking stimulus was reintroduced and thresholds measured across SOA. An SOA of ~80–90 ms is needed in the discrimination task for threshold to reach the detection threshold. ○, orientation discrimination; ▶, scene change detection.

We found that in the orientation-discrimination paradigm, a longer SOA was needed in the changing-background condition to match performance in the static-background condition. This is consistent with the hypothesis that form information is delayed when the introduction of a new local stimulus is accompanied by a change in the background (as with a saccade). At a fixed SOA, performance in the static- and changing-background conditions could be matched by using a higher bar contrast when the background changed. Contrast appears to have a significant effect in speeding up the availability of form information, specifically in a delayed representation. In the changing-background condition, a longer SOA was needed to discriminate bar orientation than to detect that the scene had changed. This suggests that with the conditions of our experiment, there is an early stimulus response that carries little form information compared with a later response. While there were notable differences, all of the results listed here were found with either a background luminance increment or a background pattern change with fixed mean luminance.

Comparisons with previous psychophysical findings

While there is a large body of psychophysical results on discrimination and detection, most experiments have been conducted using isolated visual stimuli flashed on static backgrounds. Using a backward masking paradigm, we found significant differences in perceptual thresholds in the static- and changing-background situations. The time dependence of thresholds is also quite different in the two situations with or without a background change.

Several psychophysical studies have shown that detecting the presence of a visual object is usually faster than identifying the precise features of the object (Fize et al. 2000; Keysers et al. 2001; Reynolds 1981; Thorpe et al. 1996). In studies of reaction time, simple reaction times are found approximately 100–150 ms faster than choice reaction times (see Luce 1986 for review). These findings support the notion that detection or coarse discrimination can occur faster than fine discrimination.

With large feature differences, thresholds for discrimination and detection are similar (Graham 1985; Thomas and Gille 1979; Watson and Robson 1981). This is why in our experiments we chose to use large orientation differences (30 or 90°) at which no threshold (Thomas and Gille 1979) or time course (Zlatkova et al. 2000) difference between discrimination and detection is expected. Our findings in the static-background condition are consistent with previous results. Not only did we measure similar thresholds for detection and discrimination in the static-background condition, we also found that the similarity extended over the entire range of SOAs tested. Thus with a static background, coarse orientation discrimination appears as fast as detection.

One might interpret the changing-background condition as a form of mask presented simultaneously with the stimulus bar. This raises the question whether our results might have been predicted from previous masking studies. This does not appear to be the case. For example, one might expect the threshold to be raised in the changing-background condition based on previous masking studies even when the light-plus-pattern mask we used is not a factor (see Breitmeyer 1984). Indeed, with a background pattern change, we observed a threshold increase at high SOAs (i.e., when the light plus pattern mask is so late that it does not interfere). However, there was no threshold elevation at high SOAs with a background luminance increment. Moreover, without the light-plus-pattern mask, no threshold elevation was observed with a background pattern change when the stimulus duration was >31 ms (Fig. 9*A*). Given that fixation duration in natural vision is typically approximately 200–300 ms, any masking caused by the background change resulting from a saccade probably has little effect on discrimination threshold, but it may influence the temporal aspects of discrimination.

Temporal properties of perception

The results with a changing background are in marked contrast with those obtained with a static background. With the changing background, we consistently found that discrimination is significantly delayed compared with detection of a scene change. One nuance to the data involves the nature of the detection. In the changing-background condition, the background luminance or pattern changed along with the introduction of a focal bar stimulus. Thus subjects were able to use either the bar or background change to detect a "scene change." The data do not explicitly show whether orientation discrimination would be delayed relative to detection of just the bar. However, detection of the bar would require that it be differentiated from the background, a feat that might automatically make coarse orientation discrimination possible.

It is important in thinking about the "realism" of various psychophysical experiments to note the duration of fixation prior to flashing the stimulus used for testing. When we varied the interval between the introduction of a background and the presentation of a bar, we found that when a background change preceded a local stimulus by more than ~250 ms the results were comparable to what we call the static-background condition. Such thresholds are lower than in the changing-background condition that we argue is more natural. This means that in typical psychophysical experiments in which subjects fixate for 100 ms, 200 ms, or longer before the test stimulus is presented, the thresholds are probably lower than what could be obtained with identical test stimuli in a natural situation with saccades constantly changing the background. Moreover, the availability of form information needed to make discriminations is significantly earlier in typical fixation experiments than natural vision.

Our study concerns the temporal aspects of human detection and discrimination and their relationships with how visual stimuli are introduced. In the changing-background situation, the previous visual scene before the stimulus onset is different from that in the static-background situation. From the viewpoint of visual context, this difference of scene history may exert a type of contextual influence that could affect visual perception.

Several studies have examined contextual influences on human detection and discrimination thresholds by manipulating stimuli surrounding a target stimulus. By comparing human performance with either the neuronal responses recorded from macaque V1 (Kapadia et al. 1995; Li et al. 2000) or blood-oxygen-level-dependent signals recorded from human V1 (Zenger-Landolt and Heeger 2003), these studies have found good agreement between psychophysical performance and V1 activity. Fewer attempts have been made to link the *temporal* properties of psychophysical performance with V1 activity. Nothdurft (2000, 2002) showed that detection of a pop-out target defined by orientation contrast is delayed relative to detection, and even identification, of a single target. Using a masking paradigm, Vidnyanszky et al. (2001) measured orientation discrimination thresholds of a Gabor target at different SOAs with or without other Gabor patches flanking the target. They found large contextual effects but variable effects of SOA across observers.

Our results suggest that the speed of feature discrimination is related to the way that visual stimuli are presented. Compared with the changing-background situation, discrimination is faster when a stimulus is flashed on a static background. With a static background, the stimulus onset is specific for the local stimulus itself and correspondingly, the onset of neural responses conveys important information about the stimulus features (Celebrini et al. 1993; Gawne et al. 1996; Heller et al. 1995; Müller et al. 2001; Reich et al. 2001; Vogels and Orban 1991; and our physiology results). When a stimulus is introduced simultaneously with a background change in the immediately surrounding area, the temporal onset of the visual scene is no longer specific to the local stimulus (Huang and Paradiso 2005). To segregate the new local stimulus from the overall scene change, the visual system needs extra processing time to extract stimulus feature information.

Yantis and Jonides (1984) have shown that an object appearing abruptly in a previously blank location captures attention and makes the object easily detected. In both static- and changing-background conditions, our experimental subjects viewed foveal stimuli and attended to them to perform a task. This observation argues that the difference between static- and changing-background results is not due to differences in the allocation of attention. On the surface, our results might appear to resemble change blindness in which the visual system is unable to detect large changes in a visual scene introduced during saccades, blinks, and other transients (Pashler 1988; Simons and Levin 1997; see Rensink 2002 for review). However, our findings are different in a fundamental way. In change blindness, cueing the location of the change prior to the stimulus can substantially improve sensitivity to change detection. In our experiments, the threshold differences between the changing- and the static-background conditions were observed when the stimulus bar was always cued and presented foveally.

In natural viewing conditions, saccades bring both new stimuli and backgrounds into each portion of the visual field. Previous studies have examined visual sensitivity before, during, and after saccades (Beeler 1967; Campbell and Wurtz 1978; Diamond et al. 2000; MacKay 1970; Thiele et al. 2002), but the temporal properties of discrimination and detection with stimuli brought into the visual field by saccades are not known. Given that our experiments were not conducted with free viewing of natural scenes, caution is warranted in interpreting the implications of the results for natural vision. However, as discussed in the previous paper, luminance and pattern changes in the background are the norm rather than the exception with a saccade. Thus our findings with the background luminance change and background pattern change suggest that the brain's access to form information might be delayed in natural conditions compared with what is observed in many psychophysical experiments based on fixation and the presentation of isolated stimuli.

Relationship to physiological data

The psychophysical results we have obtained are qualitatively consistent with the visual responses we recorded in macaque V1. All three predictions about human perception described in the INTRODUCTION were confirmed. Quantitatively, the timing differences measured in our human psychophysics experiments tended to be shorter than those inferred from the physiology results. For instance, with a uniform light background, the SOA difference between the static and the changing-background conditions was ~5–34 ms in the orientation discrimination paradigm (see Fig. 3). Several different measurements from the physiological experiments are interesting and relevant points of comparison. The delayed response in the changing-background condition (presumably carrying the orientation information) was ~20–50 ms later than the early response in the static-background condition (see Huang and Paradiso 2005, Figs. 4*A* and 6*B*). The difference of the peak response latency between the delayed response in the changing-background condition and the early response in the static-background condition shown in Fig. 4*A* of the companion paper is 30–50 ms; the mean response latency difference of the data shown in Fig. 6*B* is 24 ms. Another similarity between the human psychophysics and macaque physiology data is that the early/late response time difference decreased as the stimulus contrast increased. However, the relationship between contrast and timing was different in psychophysics and physiology. In the human psychophysical data, the smallest difference in SOA needed to make equivalent discriminations (5–12 ms) was found at 30% contrast (bar luminance of 17.8 cd/m^2) and the largest (~18–34 ms) was found at 14% contrast (bar luminance of 12.7 cd/m^2; see Fig. 3*A*). In the macaque physiology data, the static/changing-background condition latency difference was ~50 ms at 90% contrast, and ~70 ms at 30% contrast with a Gabor stimulus (see Huang and Paradiso 2005, Fig. 8).

In *Ideal observer analysis,* we examine one approach for quantitatively comparing psychophysical and physiological data. There are several factors that might contribute to quantitative discrepancies between the two types of data. First, in our macaque physiology studies, we have shown that the initial response of V1 neurons observed in the changing-background condition was less sensitive to stimulus features than was the delayed response in the changing-background condition or the early response in the static-background condition. Nevertheless, the initial response in the changing-background condition did sometimes show some sensitivity to stimulus form. If orientation discrimination in the changing-background condition relies on a combination of the selective delayed component and the less-selective initial response, the perceptual timing difference observed in human psychophysics could be smaller than the latency difference between the initial and the delayed neural responses. Second, visual backward masking does not "erase" all neural activity evoked by the visual stimulus (see Breitmeyer and Ogmen 2000 for review). The timing difference between the masking functions is only an approximation of the perceptual timing difference. Third, in the physiological experiments, the RFs were approximately3–6° eccentric from the fovea, and monkeys were not required to pay attention to the stimuli. In contrast, in the human psychophysics experiments, all the tasks were performed at the fovea, and subjects had to perform a threshold discrimination or detection task. Central fixation and attention may improve performance more on the harder tasks, which usually involved background changes.

From the viewpoint of sensory processing, a perceptual time delay could result from the underlying neural response having a longer latency or alternatively rising more gradually before it reaches a threshold. These two possibilities could also coexist. If neural activity sensitive to stimulus features is simply delayed, we would expect that the psychometric function for orientation discrimination in the changing-background condition would be a time-shifted version of the function for the static-background condition (i.e., the slopes across SOA would be the same). The same argument can be made for orientation discrimination and scene-change detection. With background luminance changes, these are what we observed. When varying SOA, the slopes of the psychometric functions for orientation discrimination in the changing-background condition were similar to those in the static-background condition and were slightly smaller than those for scene-change detection. In contrast, the slopes of the psychometric functions for orientation discrimination with a background pattern change were much more gradual than those with a static-pattern background (Fig. 8*B*) and those for scene-change detection (data not shown). This implies that when stimuli are introduced simultaneously with background pattern changes, the feature-selective neural response rises more slowly than that in the static-pattern background condition. This is consistent with the physiology results (see Huang and Paradiso 2005, Figs. 12*A* and 14*A*).

Scene-change detection

In recordings from V1 we found that the initial neuronal responses were relatively unselective for stimulus orientation and contrast. Many V1 neurons also showed a comparable initial response to the background change even if no bar was present. These findings suggest that the initial response signals that the scene has changed but does not carry specific information about the stimulus bar. This is why the detection task in the changing-background condition was to detect any change in the visual scene (background or bar) rather than the presence of a stimulus bar. At short SOAs (12 and 18 ms), the contrast thresholds for scene change detection were similar to those for orientation discrimination. It appears that, at these short SOAs, subjects relied on detecting the presence of the stimulus bar to detect the visual scene change; the visual scene change could not be detected based on the background luminance or pattern change alone. This is probably because, with such short SOAs, the background, bar, and mask perceptually fused and the bar was detectable in the fused percept with the mask, whereas the background was not detectable. At longer SOAs the bar was not necessary for detecting the scene change.

Ideal observer analysis

To provide a more quantitative comparison of our psychophysical and physiological data, we computed the detection and discrimination performance that would be expected of an ideal observer based on the response of neurons we studied. The procedure to calculate the performance of the ideal observer is the following. We assume that the ideal observer accumulates evidence from neuronal responses over time to make the decision for detection and discrimination. Thus we first calculate the integrated neuronal response: $R(t) = \int_0^t r(\tau)d\tau$, where $r(\tau)$ is the firing rate of the neuron at time τ.

We then calculated d' based on two integrated responses *R1* and *R2*. For orientation discrimination, *R1* is calculated based on the response to an optimally oriented stimulus for the neuron and *R2* is to an orthogonal orientation. For scene-

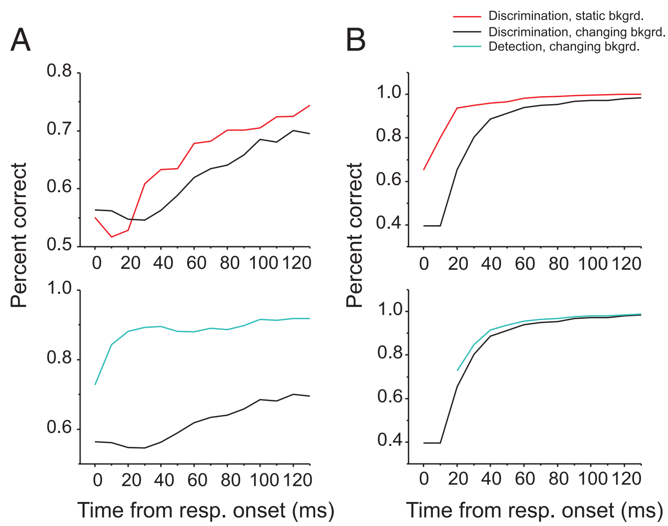

FIG. 11. Performance of an ideal observer on orientation discrimination and scene change detection based on the responses of 2 neurons. *A*: neuron from subpopulation I of the previous paper that showed a biphasic response to a stimulus bar in the changing-background condition. *B*: neuron that showed a delayed-only response to a stimulus bar in the changing-background condition (from subpopulation II). *Top*: comparison of discrimination performance in the static- and changing-background conditions. *Bottom*: comparison of detection and discrimination in the changing-background condition. To facilitate comparison with the psychophysical data in Figs. 3*B* and 6*B, time 0* is the shortest neuronal response onset time.

change detection, *R1* is based on the response to an optimally oriented stimulus introduced with a background change, whereas *R2* is the integrated null response.

$$d'(t) = \frac{|\mathrm{Mean}_{R1}(t) - \mathrm{Mean}_{R2}(t)|}{\sqrt{\frac{\mathrm{SD}_{R1}(t)^2 + \mathrm{SD}_{R2}(t)^2}{2}}},$$

where $\mathrm{Mean}_R(t)$ is the mean integrated response up to time t and $\mathrm{SD}_R(t)$ is the SD of the integrated response (see Geisler 2003).

Assuming that the neuronal response is normally distributed, in a 2AFC task, an ideal observer that uses the single neuron's response will perform with an accuracy (percent correct) of

$$\mathrm{PC}(t) = \phi\left(\frac{d'(t)}{\sqrt{2}}\right),$$

where ϕ is the standard normal integral function: $\phi(z) = \frac{1 + erf\left(\frac{z}{\sqrt{2}}\right)}{2}$, and erf is the error function: $erf(x) = \frac{2}{\sqrt{\pi}}\int_0^x e^{-t^2}dt$. A d' of 1 corresponds to 76% correct in a 2AFC task (see CBASSE 1985).

Figure 11 shows the ideal observer analysis applied to two neurons from the study reported in the previous paper. The neuron in Fig. 11*A* comes from subpopulation I and showed a biphasic response to a stimulus bar in the background luminance increment condition. The neuron in Fig. 11*B* comes from subpopulation II and showed a delayed-only response to a stimulus bar in the background luminance increment condition. The *top panels* in the figure compare discrimination performance in the static- and changing-background conditions. The ideal observer performance shown in the *top* of Fig. 11 can be compared with the psychophysical data on the *right side* of Fig. 3. In both the ideal observer and psychophysical plots, discrimination performance is generally better with the static than with the changing background. In addition, to achieve the same performance level, a longer time is needed in the changing than in the static-background condition for both the ideal observer and human performance. The ideal observer analysis shows that discrimination based on the responses of macaque V1 neurons in the changing-background condition is ~20–40 ms slower than in the static-background condition. This timing difference is in good accordance with, although slightly longer than, the human psychophysics results (~10–20 ms difference). We discussed in the preceding text the reasons why differences might be expected.

Figure 11, *bottom,* compares ideal observer detection and discrimination in the changing-background condition (compare with psychophysical data in Fig. 6*B*). In the psychophysical data, detection is ~10–22 ms faster than discrimination. For the neuron showing a biphasic response, detection performance is clearly better than discrimination; it takes a significantly longer time (>120 ms) for the discrimination performance to reach the same level as detection (Fig. 11*A*, *bottom*). For the neuron showing a delayed-only response, the difference between detection and discrimination is subtle—detection is ~3 ms faster than discrimination (Fig. 11*B*, *bottom*). This is expected as an ideal observer's performance at both discrimination and detection relies on the delayed response of the neuron, so detection is no longer significantly faster than discrimination. As information carried by both types of neurons may be pooled to guide behavior, the psychophysics performance would be expected to lie between the representative timing differences of two types of neurons shown in Fig. 11. The ideal observer analysis is in reasonable quantitative agreement with the psychophysical performance we measured.

ACKNOWLEDGMENTS

We thank T. Hanks for assistance with the experiments.

Present address of X. Huang: Keck Center, Dept. of Physiology, Univ. of California, 513 Parnassus Ave, San Francisco, CA 94143-0444.

GRANTS

This research was supported by the National Eye Institute and the Keck Foundation.

REFERENCES

Beeler GW Jr. Visual threshold changes resulting from spontaneous saccadic eye movements. *Vision Res* 7: 769–775, 1967.

Breitmeyer BG. *Visual Masking: An Integrative Approach.* New York: Oxford, 1984.

Breitmeyer BG and Ogmen H. Recent models and findings in visual backward masking: a comparison, review, and update. *Percept Psychophys* 62: 1572–1595, 2000.

Campbell FW and Wurtz RH. Saccadic omission: why we do not see a grey-out during a saccadic eye movement. *Vision Res* 18: 1297–1303, 1978.

Celebrini S, Thorpe S, Trotter Y, and Imbert M. Dynamics of orientation coding in area V1 of the awake primate. *Vis Neurosci* 10: 811–825, 1993.

Diamond MR, Ross J, and Morrone MC. Extraretinal control of saccadic suppression. *J Neurosci* 20: 3449–3455, 2000.

CBASSE (Commission on Behavioral and Social Sciences and Education). *Emergent Techniques for Assessment of Visual Performance.* Washington DC: National Academy, 1985.

Fize D, Boulanouar K, Chatel Y, Ranjeva JP, Fabre-Thorpe M, and Thorpe S. Brain areas involved in rapid categorization of natural images: an event-related fMRI study. *Neuroimage* 11: 634–643, 2000.

Gawne TJ, Kjaer TW, and Richmond BJ. Latency: another potential code for feature binding in striate cortex. *J Neurophysiol* 76: 1356–1360, 1996.

Geisler WS. Ideal observer analysis. In: *The Visual Neurosciences*, edited by Chalupa L and Werner J. Boston: MIT Press, 2003, p. 825–837.

Graham N. Detection and identification of near-threshold visual patterns. *J Opt Soc Am A* 2: 1468–1482, 1985.

Heller J, Hertz JA, Kjaer TW, and Richmond BJ. Information flow and temporal coding in primate pattern vision. *J Comput Neurosci* 2: 175–193, 1995.

Huang X, Blau S, and Paradiso MA. Aspects of human detection and discrimination correlate with macaque V1 physiology (Abstract). *Vis Sci Soc J Vision* 1: 201a, 2001.

Huang X and Paradiso MA. Background changes delay information represented in macaque V1 neurons. *J Neurophysiol* 94: 4331–4343, 2005.

Kapadia MK, Ito M, Gilbert CD, and Westheimer G. Improvement in visual sensitivity by changes in local context: parallel studies in human observers and in V1 of alert monkeys. *Neuron* 15: 843–856, 1995.

Keysers C, Xiao DK, Foldiak P, and Perrett DI. The speed of sight. *J Cogn Neurosci* 13: 90–101, 2001.

Li W, Thier P, and Wehrhahn C. Contextual influence on orientation discrimination of humans and responses of neurons in V1 of alert monkeys. *J Neurophysiol* 83: 941–954, 2000.

Luce RD. Response times: their role in inferring elementary mental organization. In: *Oxford Psychology Series.* Oxford Univ Press, 1986.

Mackay DM. Elevation of visual threshold by displacement of retinal image. *Nature* 225: 90–92, 1970.

Müller JR, Metha AB, Krauskopf J, and Lennie P. Information conveyed by onset transients in responses of striate cortical neurons. *J Neurosci* 21: 6978–6990, 2001.

Nothdurft HC. Salience from feature contrast: temporal properties of saliency mechanisms. *Vision Res* 40: 2421–2435, 2000.

Nothdurft HC. Latency effects in orientation popout. *Vision Res* 42: 2259–2277, 2002.

Pashler H. Familiarity and visual change detection. *Percept Psychophys* 44: 369–378, 1988.

Reich DS, Mechler F, and Victor JD. Temporal coding of contrast in primary visual cortex: when, what, and why. *J Neurophysiol* 85: 1039–1050, 2001.

Rensink RA. Change detection. *Annu Rev Psychol* 53: 245–277, 2002.

Reynolds RI. Perception of an illusory contour as a function of processing time. *Perception* 10: 107–115, 1981.

Simons DJ and Levin DT. Change blindness. *Trends Cogn Sci* 1: 261–267, 1997.

Thiele A, Henning P, Kubischik M, and Hoffmann KP. Neural mechanisms of saccadic suppression. *Science* 295: 2460–2462, 2002.

Thomas JP and Gille J. Bandwidths of orientation channels in human vision. *J Opt Soc Am* 69: 652–660, 1979.

Thorpe S, Fize D, and Marlot C. Speed of processing in the human visual system. *Nature* 381: 520–522, 1996.

Vidnyanszky Z, Papathomas TV, and Julesz B. Contextual modulation of orientation discrimination is independent of stimulus processing time. *Vision Res* 41: 2813–2817, 2001.

Vogels R and Orban GA. Quantitative study of striate single unit responses in monkeys performing an orientation discrimination task. *Exp Brain Res* 84: 1–11, 1991.

Watson AB and Robson JG. Discrimination at threshold: labelled detectors in human vision. *Vision Res* 21: 1115–1122, 1981.

Yantis S and Jonides J. Abrupt visual onsets and selective attention: evidence from visual search. *J Exp Psychol Hum Percept Perform* 10: 601–621, 1984.

Zenger-Landolt B and Heeger DJ. Response suppression in v1 agrees with psychophysics of surround masking. *J Neurosci* 23: 6884–6893, 2003.

Zlatkova M, Vassilev A, and Mitov D. Temporal characteristics of line orientation identification. *Percept Psychophys* 62: 1008–1018, 2000.