



Two distinct modes of sensory processing observed in monkey primary visual cortex (V1)

Hans Supèr^{1,2}, Henk Spekreijse¹, Victor A. F. Lamme^{1,2}

¹ Graduate School of Neurosciences, Department of Visual System Analysis, AMC, University of Amsterdam, PO Box 12011, 1100 AA Amsterdam, The Netherlands

² The Netherlands Ophthalmic Research Institute, Meibergdreef 49, 1105 BA Amsterdam, The Netherlands

Correspondence should be addressed to V.A.F.L. (v.lamme@amc.uva.nl)

Even salient sensory stimuli are sometimes not detected. What goes wrong in the brain in that case? Here we show that a late (> 100-ms) component of the neural activity in the primary visual cortex of the monkey is selectively suppressed when stimuli are not seen. As there is evidence that this activity depends on feedback from extrastriate areas, these findings suggest a specific role for recurrent processing when stimuli are reaching a perceptual level. Further results show that this perceptual level is situated between purely sensory and decision or motor stages of processing.

Presented sensory stimulation are sometimes detected, and sometimes not detected, depending on a number of variables. The more salient a stimulus, the higher the likelihood that it will be detected¹. The internal state of the subject that is detecting the stimulus is also of critical importance: sensory processing will not be identical for the same physical stimulus on every occasion². Moreover, sensory processing is followed by a decision stage, during which the internal representation of the stimulus has to pass the subjects' perhaps variable criterion for a response to be given^{3–8}. Here we recorded from the primary visual cortex of awake monkeys engaged in a task in which they indicated whether a figure on a background was or was not present. We used highly salient stimuli that were only occasionally missed. Early transients of the responses of V1 neurons did not differ for stimuli that were perceived and those that were not perceived. However, a response component that selectively signals figure-ground segregation—contextual modulation^{9,10}—was selectively and fully suppressed when high saliency stimuli were not seen.

We further investigated the involvement of this delayed activity in the cascade of information processing that occurs between the presentation of a stimulus and the behavioral response, by manipulating stimulus saliency and response criterion. This showed that the modulation is neither a direct representation of the stimulus nor a direct reflection of the outcome of the decision process. The data suggest the existence of an intermediate stage of sensory processing that may operate in two different modes, reflecting whether the stimulus has or has not reached a 'perceptual' level of processing.

RESULTS

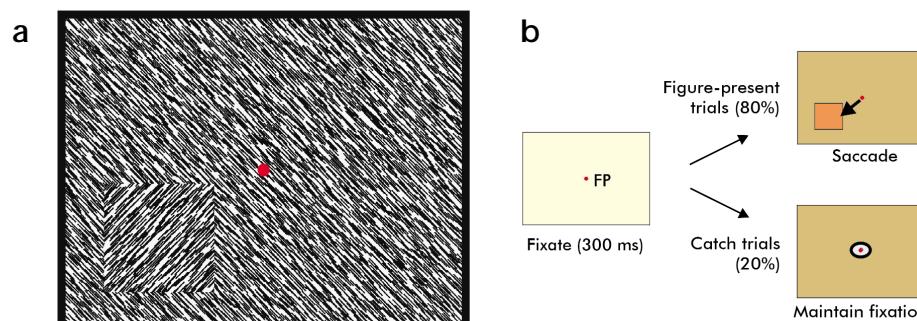
Behavior

To have monkeys report whether stimuli were perceived or not, we used a previously described protocol¹¹. The animals (two *Macaca mulatta*) were trained to fixate on a central red dot (size, 0.2°) of an otherwise black and white computer display. After

having fixated for 300 ms, the stimulus screen appeared (Fig. 1a), consisting of a texture made of oriented line segments. In 'figure-present' trials, a small square region, with line segments of orthogonal orientation, was present in the display (Fig. 1a). This square figure could appear at one out of three possible locations (Fig. 2a), and the monkey had to make a saccadic eye movement toward it within 500 ms to obtain a reward. In 'catch' trials (20%), a texture screen appeared as well, but without a figure. On those trials, the monkey was rewarded when it maintained fixation for 500 ms (Fig. 1b). In this way, the monkey could report either that he perceived or that he did not perceive a figure.

Analysis of the animals' eye movements in this task (Fig. 2a) revealed that on most figure-present trials, the animal made a correct saccade toward the target window. Also, most catch trials resulted in the correct maintenance of fixation. In total, both animals made a correct saccade in 78% of the figure-present trials and maintained fixation in 88.1% of catch trials. This indicates that the animals were well able to detect the figure. Nevertheless, on some figure-present trials, the animal maintained fixation (Fig. 2a), as if he judged that a catch trial was presented instead. In total, this happened in 8.1% of cases. We classified the figure-present trials as 'seen' when the animal made a correct saccade, and as 'not seen' when the monkey maintained fixation (the words 'seen' and 'not seen' are only intended as a short denominator, a relationship with the animals internal experience is not implied; see also below). The remaining 13.9% of figure-present trials could not be straightforwardly classified (Fig. 2a); on some occasions the saccade was just too short to reach the target window, and on other occasions it was in the wrong direction altogether. Of the latter, only a few were in the direction of the other possible figure positions. Also, the 11.9% of catch trials in which the animals did not correctly maintain fixation were not further classified. Mostly, the animals did not maintain fixation accurately enough (Fig. 2a). The saccades made were typically not in the direction of a possible figure location. To avoid mixing up trials with possibly different or ambiguous interpretations, these other sets of trials were not analyzed.

Fig. 1. Figure-ground display and sequence of visual stimulation. (a) A difference in orientation (90°) of line segments results in a textured figure-ground display. Here, line length is 16 pixels (L16); in this study, shorter line segments were used as well. (b) Animals had to fixate at a central point (FP). At stimulus onset, a textured display (brown) appeared with a figure (orange) in one of three possible locations (figure-present trials). The animals had to make a saccade toward the figure (arrow) within 500 ms to obtain a reward. In some trials (catch trials) a texture without figure appeared. In that case, the animals had to maintain fixation during 500 ms (open circle).



While the animals were engaged in this task, multi-neuron activity in V1 was recorded through chronically implanted microwire electrodes^{12,13}. We positioned the stimuli such that one of the three figure positions was centered on the (much smaller) receptive fields of the V1 neurons (Fig. 3a). When the square appeared at this position, we recorded responses to 'figure.' When the square appeared at another location, responses to

the background ('ground') were obtained. We presented trials in which the figure lines had a 135° orientation, and the background lines had a 45° orientation, as well as trials in which the figure elements were at 45° and the background at 135° . Responses to these two complementary stimuli were averaged^{12,13}. In this way, the receptive field stimulation was identical for the 'figure' and the 'ground' responses.

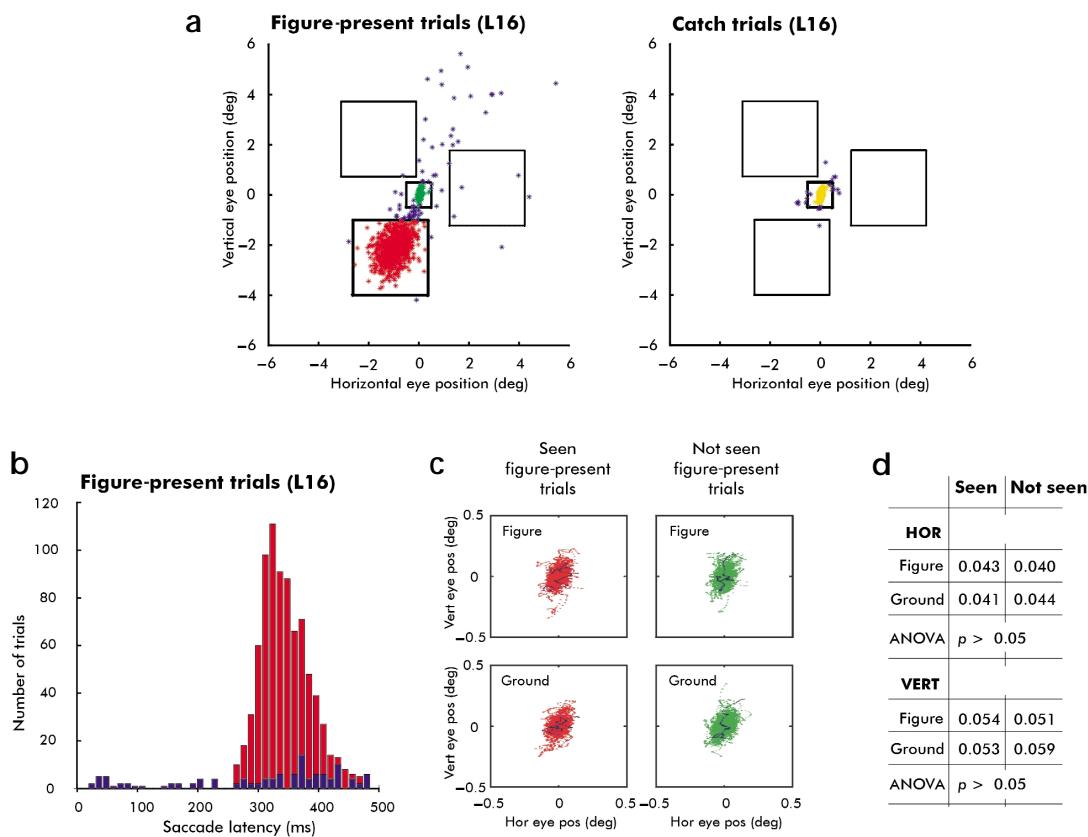


Fig. 2. Eye movements. (a) Positions of endpoints of saccades (red, blue) or fixations (green, yellow) for figure-present trials in which the lower left figure was presented (left panel) and catch trials (right panel). Thin line boxes, possible figure positions; thick line box, target figure. Central box, fixation window. Data are from monkey Uri, for the L16 experiment. (b) Latencies of the saccades that are shown in Fig. 2a, relative to stimulus onset in figure-present trials. Correct saccades toward the target figure are shown in red; erroneous saccades are shown in blue. (c) Examples of eye positions from 0–240 ms after stimulus onset (dark blue), superimposed on 50 random other similar fixations. Fixation patterns are separated according to the conditions 'seen' (red), 'not seen' (green), figure (top) and ground (bottom). Axes are the size of the fixation window. (d) Average standard deviations of the eye x- and y-positions during the interval 0–240 ms, for the conditions 'seen,' 'not seen,' figure and ground. Differences are not significant.



Fig. 3. Receptive fields, stimuli and neural responses. (a) Aggregate receptive fields of the 16 multi-neuron recording sites in each monkey (circles). Red circles indicate receptive fields from which significant contextual modulation is obtained. Squares indicate the possible locations of figures; the central square depicts the fixation window. (b) Average neural responses to figure and ground stimulation from a typical electrode site. Gray shading, contextual modulation. (c) Strength of average neural response (100–240 ms) to figure plotted against neural response strength for background. Each dot represents an individual recording site. Red dots indicate a significant ($p < 0.05$) difference between the two responses; blue dots, non-significant differences.

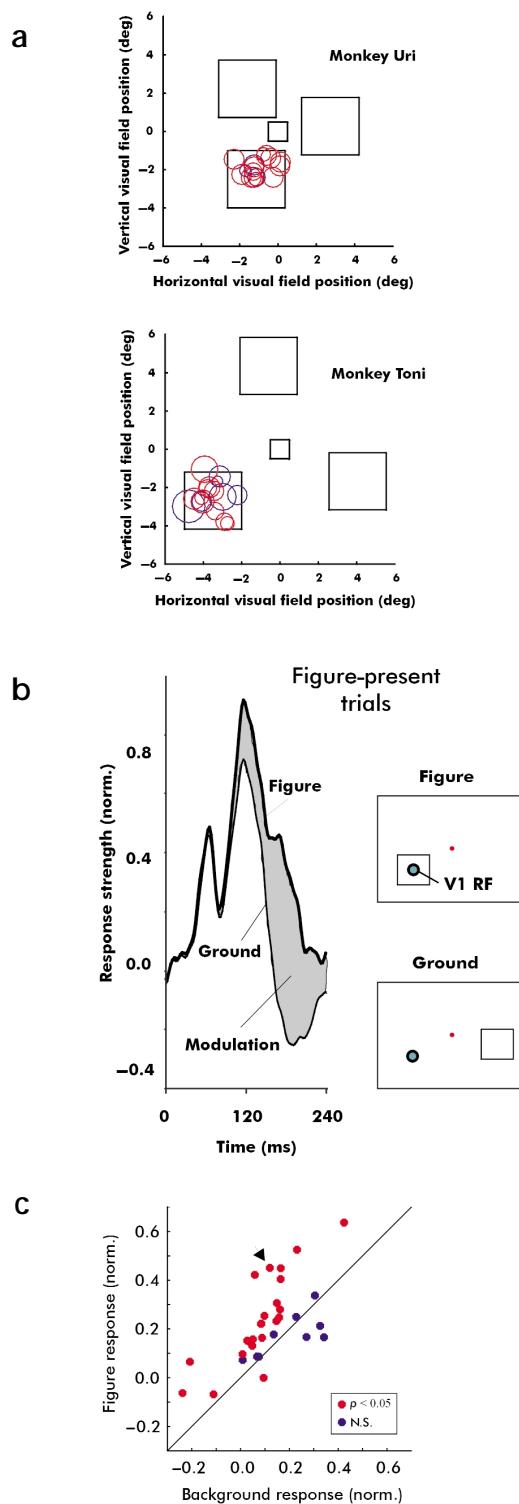
The animals were free to make a saccade as soon as the stimulus screen appeared. This allowed the possibility of saccadic eye movements contaminating the responses. Most of the correct saccades to the figure were initiated later than 240 ms after stimulus onset (Fig. 2b). The saccades started earlier were mostly erratic, and we discarded those trials. Furthermore, we only analyzed the neural activity during the interval from 0 to 240 ms after stimulus onset, to avoid any contamination of the neural activity by saccades. A second potential concern was that somehow, the positions or movements of the eyes could differ in some subtle respect before the monkey left the fixation window and that this caused differences in response. To control for such differences in fixation behavior, we separated the eye movements according to stimulus and response type (figure, ground, seen, not seen), and analyzed the interval from 0–240 ms. We calculated the standard deviation of the x and y coordinates of the eye position during each trial. The higher this value, the less accurate fixation was maintained. Examples of the four types of fixations are shown in dark blue in Fig. 2c, superimposed on 50 randomly chosen other fixations of the same type. The average standard deviations for the four types of trials were not different (Fig. 2d). This result shows that any difference in neural response that was obtained, between either figure and ground, or between 'seen' and 'not seen' trials could not be attributed to differences in eye movements before the saccade. This confirmed our earlier analyses, and controls on the (lack of an) involvement of eye movements in responses obtained with these stimuli^{9,10,12,13}.

Neural activity, contextual modulation

Average neural responses to figure and ground texture, obtained at a typical electrode site (Fig. 3b) were the same up to about 90 ms, but then were stronger for figure than for ground. We refer to this phenomenon as contextual modulation (gray area, Fig. 3b). This kind of modulation specifically represents figure-ground segregation in a variety of conditions^{9,10,13}, and is only present in the awake animal¹². It belongs to a broader class of modulatory effects^{14,15} related to various perceptual phenomena like pop-out^{16,17} or perceptual grouping^{18,19}, and also reflects aspects of perceptual illusions^{20,21}. Cortico-cortical feedback²² is probably important in the generation of contextual modulation^{23–25}. Of the 32 recorded sites, we continued our analysis with the 23 that showed significant ($p < 0.05$) modulation (22 positive, 1 negative modulation, Fig. 3c; population average, Fig. 4a).

Neural activity, 'seen' versus 'not seen'

In 8.1% of figure-present trials, the monkeys did not report to have seen the figure. Therefore, we were able to investigate the role of contextual modulation and of V1 activity in general in the perception of figure from ground. We analyzed the neuronal activities of 'seen' and 'not seen' trials separately (Fig. 4b). In both conditions, a clear neural response could be observed. This indicates that, to a large extent, the V1 activity was identical for stimuli that were detected or not. However, an important and qualitative difference was observed between the 'seen' and 'not seen' conditions when we focused on the amount of contextual modulation that was evoked (Fig. 4b). Such modulation was present when the figure was 'seen,' and absent when the figure was 'not seen.' This result indicates that contextual modulation signals fig-



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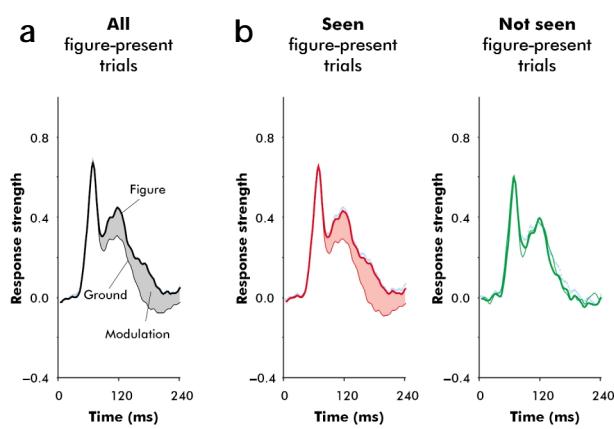


Fig. 4. 'Seen' versus 'not seen' neural responses. (a) Population average neural response to the figure-present trials with line length L16. The difference between the response to figure (thick line) and ground (thin line) is shaded. Standard error of the mean is plotted as dots (blue) above the figure response. (b) Figure and ground responses for 'seen' (red) and 'not seen' (green) figure-present trials separately. Other designations as in (a).

ure-ground relationships when the animals detect the figure, and that modulation is absent when the figure is not detected. As contextual modulation probably depends heavily on horizontal and feedback connections^{22–25}, this suggests that recurrent processing is selectively impaired when an otherwise salient stimulus is occasionally not perceived. These data thus argue for a specific role of recurrent processing in perception.

Manipulating saliency

The data leave open the question of how the modulation is related to the whole cascade of visuomotor transformations that occur in a task like this^{3–8}. The modulation develops well before the saccade, and it could be related to a purely sensory process, to a neural process involved in the preparation or execution of the saccade²⁶, or to anything in between^{4,5}.

To further explore this, we altered the figure-ground textures by shortening the line segments using not only 16 pixels, as in the experiments thus far, but also 8, 4 or 2 pixels (L16 to L2, Fig. 5a). This resulted in a significant decline of the detectability of the figure²⁷, the 'seen'/'not seen' ratio dropped (to almost zero for L2), whereas the performance for catch trials remained more or less consistent (Fig. 5b). Neural activity evoked by these stimuli is shown in Fig. 5c. Contextual modulation was most prominent for the most salient stimulus (L16), and declined with less salient figure-ground displays (L8, L4). For the L2 stimulus, no modulation was observed at all. Also, there seemed to be a difference in latency of modulation for the different types of stimuli. To quantify these (and further) effects, the mean strength of contextual modulation was calculated by subtracting the ground response from the figure response during the interval between 100 and 240 ms (Fig. 5d). Modulation was largest for the L16 stimulus, decreased with shorter line segments, and was absent for L2 (difference between all pairs $p < 0.01$). The stimulus-evoked modulation thus correlated very well with the detectability of the figures.

We again classified the electrophysiological data into 'seen' and 'not seen'. For the L2 stimulus, there were too few 'seen' trials to be analyzed in this way. Responses to figure were always lower when the figure was 'not seen' compared to when it was

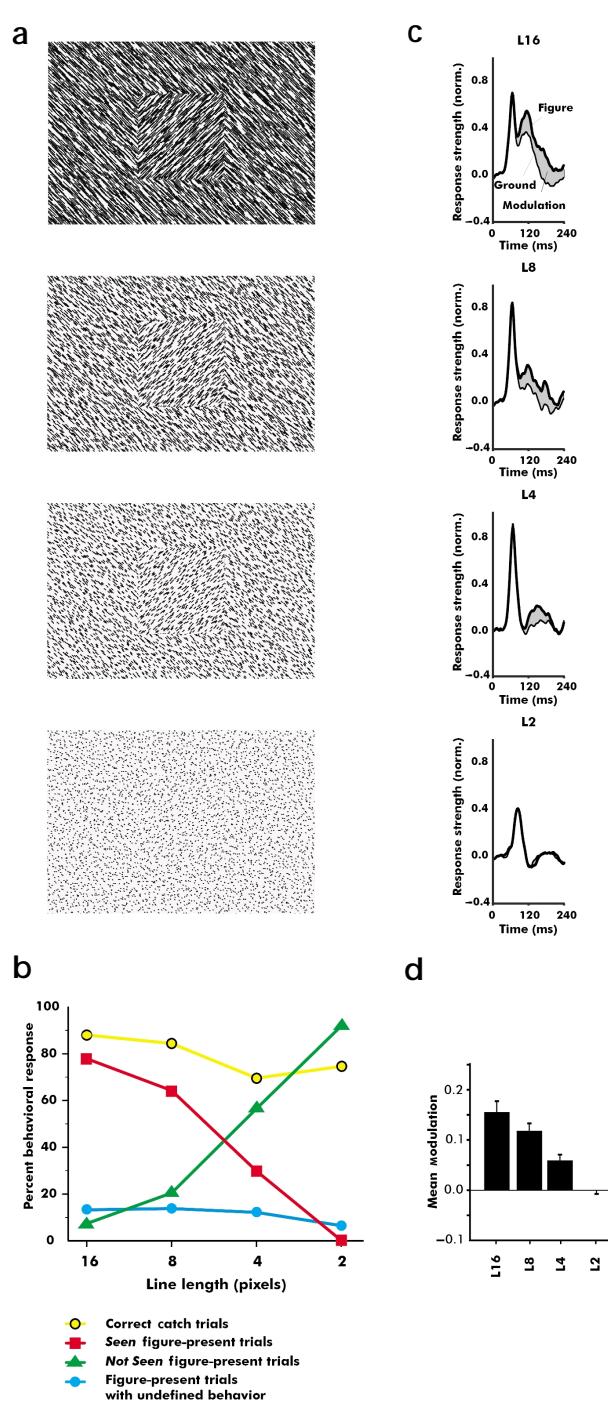


Fig. 5. Different line lengths, perceptual saliency and contextual modulation. (a) Examples of figure-ground displays with different line lengths (L16–L2). In the actual experiments, backgrounds were much larger, and the figure was not presented centrally. (b) Percentage of 'seen' figure-present trials (red circles; all pairs, $p < 0.05$), 'not seen' figure-present trials (green; all pairs, $p < 0.05$), correct catch trials (yellow; all pairs, $p > 0.05$), and trials with undefined behavior (blue; all pairs, $p > 0.05$) as a function of line length of the texture stimuli. (c) Population average neural responses to figure and background stimuli of different line lengths (L16–L2). (d) Population mean strength of contextual modulation as a function of line length.

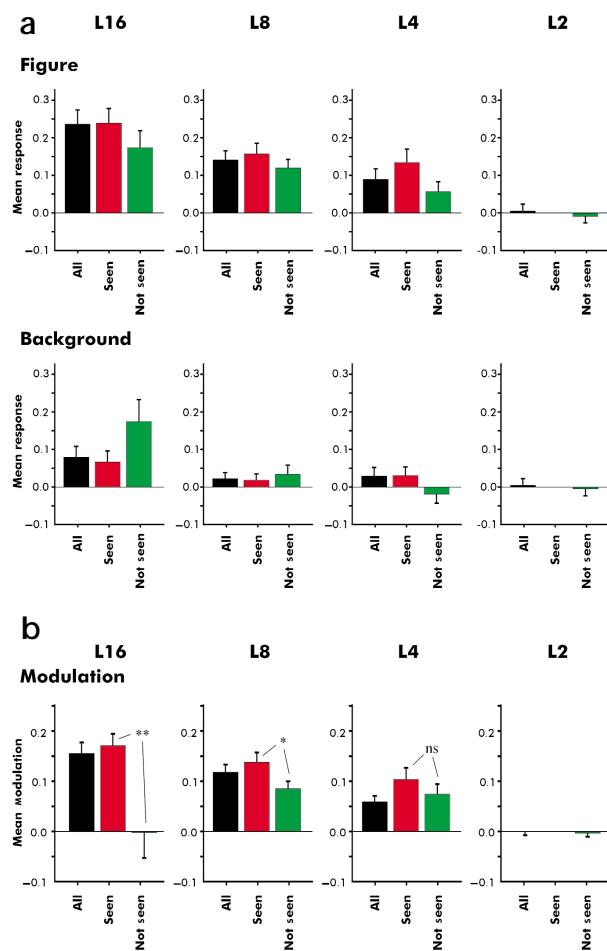


Fig. 6. ‘Seen’ versus ‘not seen’ neural responses for different levels of stimulus saliency. **(a)** Population mean response strength (100–240 ms) for figure and background, for all (black), ‘seen’ (red) and ‘not seen’ (green) figure-present trials. Vertical ticks, s.e.m. **(b)** Strength of contextual modulation as a function of line length, for all (black), ‘seen’ (red) and ‘not seen’ (green) figure-present trials. Vertical ticks, s.e.m. Asterisks, significant ($**p < 0.005$, $*$ $p < 0.05$) differences; ns, not significant. Results were obtained during the same experiments that yielded the behavioral results displayed in Fig. 5b. Black bars also include ‘trials with undefined behavior’.

‘seen’ (Fig. 6a). Responses to background showed a mixture of effects. The resultant amount of modulation is shown in Fig. 6b. As we already qualitatively showed (Fig. 4b), for the L16 stimulus there was an all-or-nothing dependence of the modulation on whether the monkey classified the trial as ‘seen’ or ‘not seen’. For the L8 stimulus this dependence was less strong, yet still significant. For the L4 stimulus, however, modulation was not significantly different for the ‘seen’ or the ‘not seen’ trials.

These data bring us one step closer toward understanding what process is reflected by contextual modulation in this task. In the L4 experiment, modulation was present in both ‘seen’ and ‘not seen’ trials. Thus, the modulation does not reflect the outcome of the decision process itself^{3–8} (‘seen’ or ‘not seen’), nor can it be neural activity related to the preparation or execution of the saccade the monkey uses to identify stimuli as ‘seen.’ In other words, the

modulation is neural activity that is on the sensory rather than on the motor side of the sensori-motor decision process^{4,5}. Similarly, the modulation cannot be a reflection of the attention that is drawn by the stimulus^{28,29}, as ‘seen’ stimuli would draw more attention than ‘not seen’ stimuli at all levels of saliency. Moreover, attention does not modulate V1 responses before 200–250 ms under conditions where the to be attended object is not *a priori* known (R. Landman, V. A. F. Lamme and H. Spekreijse, *Invest. Ophthalmol. Vis. Sci.* **40** (Suppl.) S200, 1999)³⁰. The L16 and L8 results also strongly show, however, that the modulation is not a signal that is determined by the stimulus only. Rather, it seems to reflect some internal representation of the stimulus that may function as an intermediate between strictly sensory and decision-related processes.

Modeling the sensori-motor transformation

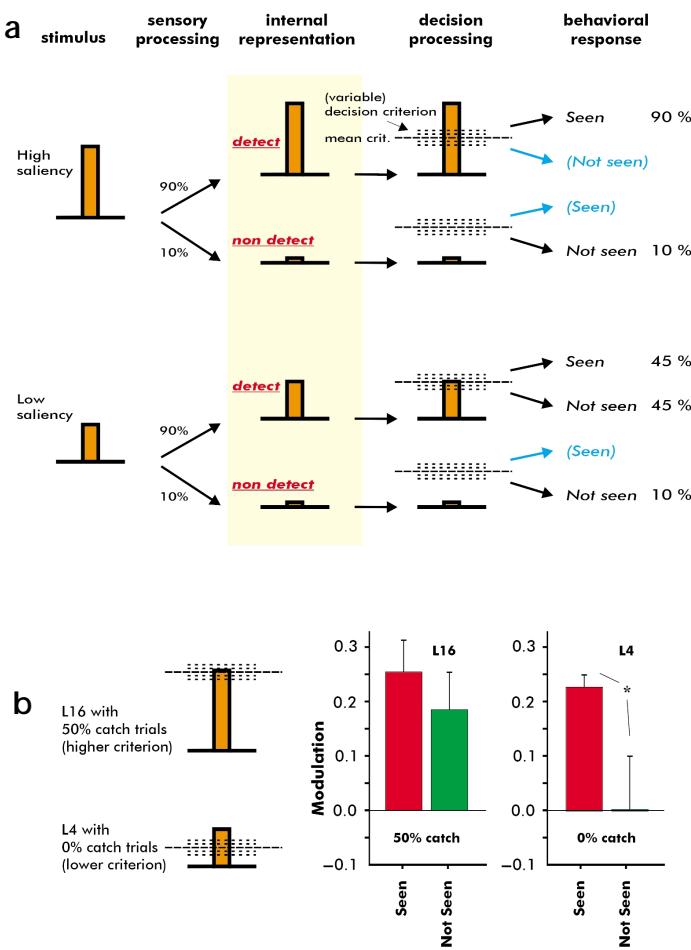
A formal representation of this argument would be a Gaussian distribution model^{1,3–8} of sensory processing followed by a decision stage³¹, with an element of two-state threshold detection theory¹ added to the sensory part (Fig. 7a). In this model, the stimulus saliency is neurally reflected in the strength of an ‘internal representation’ signal. We propose that stimuli are normally (say, 90% of cases) processed so that this signal is a veridical representation of the stimulus saliency. We refer to this mode of sensory processing as the ‘detect’ mode. However, in some cases (say, 10%), some factors (presumably inherent to the state of the brain at the moment the stimulus arrives²) cause the internal representation not to be generated. This is the ‘non detect’ mode of processing. The resulting perceptual signal is passed on to a decision stage, where it is compared to a response criterion; when the signal is above it, a ‘seen’ response follows, otherwise a ‘not seen’ response is given.

Obviously, stimuli having undergone the ‘non detect’ mode will always produce a ‘not seen’ response. High-saliency stimuli, when processed in the ‘detect’ mode, will always pass the criterion. For these stimuli, a perfect correspondence exists between the ‘seen’/‘not seen’ categorization and the ‘detect’/‘non detect’ modes. Low-saliency stimuli, on the other hand, even when processed in the ‘detect’ mode, may result in either a ‘seen’ or a ‘not seen’ response. This is because the internal signal is very close to the response criterion, and some variability in the signal strength (or alternatively in the level of the criterion) will cause it to sometimes pass and sometimes not pass the criterion. Therefore, for low saliency stimuli, the correspondence between ‘seen’/‘not seen’ and ‘detect’/‘non detect’ is lost. When we consider contextual modulation to be the ‘internal representation’ signal of Fig. 7a (yellow shaded box), the model fully explains why highly salient stimuli give a clear difference in modulation for ‘seen’ versus ‘not seen’ trials, whereas this difference disappears for low saliency stimuli (Fig. 6b).

Manipulating response criterion

The model is not only a valid way of interpreting the data; it gives a prediction that we were able to test. Experiments thus far were done with 20% catch trials, and the identical performance of catch trials for all textures (Fig. 5b) indicates that the animals’ response criterion remained constant¹. The model predicts that if the response criterion were set at a higher level, the signal from the L16 stimulus, when processed in the ‘detect’ mode, would be closer to the criterion (Fig. 7b). The situation would then become more similar to the L4 stimulus, and the difference in modulation between ‘seen’ and ‘not seen’ trials would become smaller or disappear. Similarly, lowering the criterion should bring the

Fig. 7. Model and supporting evidence of stimulus and decision processing in the visual system, showing two distinct modes of sensory processing. (a) Schematic of the model. See text for details. (b) Verification of the model, which predicts that elevating the criterion for high saliency stimuli should decrease the difference between 'seen' and 'not seen' modulation, whereas lowering the criterion for low saliency stimuli should increase this difference. Shown are the strengths of contextual modulation for 'seen' (red bars) and 'not seen' trials (green bars) for L16 stimuli presented with 50% catch trials, and for L4 stimuli with 0% catch trials (* $p < 0.05$).



L4 stimulus more frequently above criterion, and the difference in modulation for 'seen' and 'not seen' trials should become larger. To manipulate the response criterion, we changed the percentage of catch trials for L16 and L4 stimuli and recorded the responses again (Fig. 7b). Increasing the number of catch trials to 50% for the L16 stimulus indeed elevated the criterion, as is shown by the increase in catch trial performance (92.2%). In accordance with the model prediction, modulation was now present both in 'seen' and 'not seen' trials. Similarly, in the L4 experiment with 0% catch trials, contextual modulation for 'seen' versus 'not seen' trials was clearly different. These control experiments thus validate our model of the neural processes that occur while the monkeys perform this task.

DISCUSSION

We show that figure-ground contextual modulation in V1 is influenced strongly by whether stimuli are either 'seen' or 'not seen' (Fig. 4b). However, a close correspondence between the 'seen'/'not seen' categorization and the presence/absence of modulation is only found at high saliency (Fig. 6b). A model that can explain these results, and that is corroborated by additional experiments (Fig. 7), suggests that the contextual modulation is a reflection of a stage of sensory processing that is to some extent both independent of sensory input as well as of perceptual decision processing.

At this stage, stimuli may either be 'detected' or 'not detected' (Fig. 7a), presumably depending on the internal state of the visual system at the moment the stimulus arrives. These two distinct modes of sensory processing are not observed in the V1 activity preceding the contextual modulation. Both 'detected' and 'non detected' stimuli evoke similar early neuronal activity (Fig. 4b). In both cases, the visual input thus reaches V1 and produces a clear neural response. Only the contextual modulation reflects in a qualitative manner whether the stimulus has been processed up to the level of 'detection.' In other words, the two modes are not comparable to 'eyes open' and 'eyes closed.' Instead, the difference between 'detect' and 'non-detect' seems to be similar to the difference we observed between the awake and anaesthetized monkey: V1 receptive field tuning properties like orientation or direction tuning are not different between the awake and anesthetized conditions, whereas contextual modulation is fully and selectively suppressed by (isoflurane) anesthesia¹² (but see ref. 32). Therefore, the 'non detect' mode we describe here can be considered to be something like 'anesthesia in the awake.' The exact nature and origin of this state remains to be investigated, but it might be comparable to a state of inattention³³, absent-mindedness³⁴ or unawareness, albeit in a manner different from a failure to report about stimuli³⁵.

METHODS

Stimulus presentation and behavioral control. Stimuli were presented on a 21-inch monitor screen driven by TIGA software. The monkey was seated in a primate chair, and placed in a dark room 75 cm from the monitor screen ($28^\circ \times 21^\circ$ of visual angle; resolution 1024×768 pixels; refresh rate, 72.34 Hz.). In each trial, a red fixation dot (0.2°) popped up in a prestimulus texture consisting of randomly oriented line segments. After the monkey had fixated this dot for 300 ms (that is, entered and did not leave a $1^\circ \times 1^\circ$ fixation window) the stimulus texture appeared, consisting of line segments of 16, 8, 4 or 2×1 pixels ($0.44^\circ, 0.22^\circ, 0.11^\circ$ or $0.055^\circ \times 0.027^\circ$), with a density of 5 line segments per square degree. Line segments could have 45° or 135° orientation. In figure-present trials, a square of 3° was randomly chosen at one out of three possible location with an eccentricity of 2.74° – 4.4° from the fixation point. Line segments within this square region had an orientation orthogonal to that of the remainder of the screen. The result was a scene in which a square figure was perceived on a background (Fig. 1a). On catch trials, all line segments had the same orientation, so no figure was visible. In both types of trials, both orientations were used for both figure and background, resulting in 'complementary' stimulus pairs^{9,12,13}.

To obtain a juice reward in figure-present trials, the monkeys had to make a saccadic eye movement toward the figure within 500 ms after stimulus onset. When saccades landed within the region of the figure, trials were categorized as 'seen', otherwise they were considered incorrect ('undefined behavior,' Figs. 2 and 5b). When the monkey maintained fixation for 500 ms after stimulus onset, the trial was categorized as 'not seen.' To obtain a reward in catch trials, the animal had to maintain fixation for 500 ms after stimulus onset ('correct catch trials,' Fig. 5b). Eye movements were monitored using scleral search coils with the double magnetic induction method³⁶, and digitized at 400 Hz.



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Data recording and analysis. Neural activity was recorded during several sessions. Sessions with the same percentage of catch trials, but with different line lengths, were intermingled (blocked). Before each recording, animals were customized to the task (line lengths and percentage of catch trials). Results for each condition (that is, L16 to L2, Figs. 4–6, or different percentages of catch trials, Fig. 7b) are based on about 1000 to 3000 trials per monkey, obtained in about 35 sessions per monkey. Multi-neuron activity was recorded through 16 microwire electrodes in each monkey. About 40 were surgically implanted into the operculum of area V1, and 16 were selected on the basis of quality of the MUA signal and convenience of the receptive field position^{12,13}. Before the experiments, aggregate receptive field size and position at each electrode was determined using moving bars. Receptive field size ranged from 0.55° to 1.7° (median 1.0°), eccentricity from 1.3° to 2.8° in one monkey and from 3.4° to 5.7° in the other. Orientation selectivity was moderately expressed by these electrodes (mean ratio, ~2.0), and recording sites could typically be driven from either of the two eyes. Strong ocular dominance, as has been reported for layer 4C cells, is usually absent^{12,13}. Taking the RF sizes, tuning ratio and ocular dominance together, we concluded that these electrodes sampled neuronal activity over a distance of about 200–300 μm. For each monkey, figure positions and electrodes were chosen such that the figures covered the receptive fields of 16 electrodes simultaneously. Signal processing was otherwise as described before. Likewise, to have each electrode contribute equally to the population means, we used normalized responses, as described before^{12,13}. This procedure does not affect any relative difference between conditions or line lengths.

Electrophysiological data obtained during the interval between stimulus onset and 240 ms after stimulus onset was analyzed. To have receptive field stimulation the same for figure and background responses, the responses to the complementary stimulus pairs (see above) were averaged^{9,12,13}. Response strength was calculated as the average normalized activity during a 100–240 ms interval. Contextual modulation was calculated by subtracting the background response strength from the figure response strength. For the analyses of Figs. 4–6, those electrode sites were included that showed significant ($p < 0.05$) positive or negative modulation for the L16 condition (23 of the 32, Fig. 3). In general, sites that did not show significant modulation for the L16 condition also did not show significant modulation for the L8 or L4 condition (with the exception of 4 cases). For the analysis of Fig. 7b, which is based on a separate set of experiments, electrode sites were included that showed significant modulation for that condition. Typically, modulation is equally present for both orientations used. For all statistics, *t*-tests were applied.

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- Green, D. M. & Swets, J. A. *Signal Detection Theory and Psychophysics* (Wiley, New York, 1966).
- Arieli, A., Sterkin, A., Grinvald, A. & Aertsen, A. Dynamics of ongoing activity: explanation of the large variability in evoked cortical responses. *Science* **273**, 1868–1871 (1996).
- Shadlen, M. N. & Newsome W. T. Motion perception: seeing and deciding. *Proc. Natl. Acad. Sci. USA* **93**, 628–633 (1996).
- Leon, M. I. & Shadlen, M. N. Exploring the neurophysiology of decisions. *Neuron* **21**, 669–672 (1998).
- Schall, J. D. & Bichot, N. P. Neural correlates of visual and motor decision processes. *Curr. Opin. Neurobiol.* **8**, 211–217 (1998).
- Platt, M. L. & Glimcher, P. W. Neural correlates of decision variables in parietal cortex. *Nature* **400**, 233–238 (1999).
- Kim, J.-N. & Shadlen, M. N. Neural correlates of a decision in the dorsolateral prefrontal cortex of the macaque. *Nat. Neurosci.* **2**, 176–185 (1999).
- Thompson, K. G. & Schall, J. D. The detection of visual signals by macaque frontal eye field during masking. *Nat. Neurosci.* **2**, 283–288 (1999).
- Lamme, V. A. F. The neurophysiology of figure-ground segregation in primary visual cortex. *J. Neurosci.* **15**, 1605–1615 (1995).
- Zipser, K., Lamme, V. A. F. & Schiller, P. H. Contextual modulation primary visual cortex. *J. Neurosci.* **16**, 7376–7389 (1996).
- Moore, T., Rodman, H. R., Repp, A. B. & Gross C. G. Localization of visual stimuli after striate cortex damage in monkeys: parallels with human blindsight. *Proc. Natl. Acad. Sci. USA* **92**, 8215–8218 (1995).
- Lamme, V. A. F., Zipser, K. & Spekreijse, H. Figure-ground activity in primary visual cortex is suppressed by anaesthesia. *Proc. Natl. Acad. Sci. USA* **95**, 3263–3268 (1998).
- Lamme, V. A. F., Rodriguez, V. & Spekreijse, H. Separate processing dynamics for texture elements, boundaries and surfaces in primary visual cortex. *Cereb. Cortex* **9**, 406–413 (1999).
- Allman, J. M., Miezin, F. & McGuiness, E. Stimulus specific responses from beyond the classical receptive field: Neurophysiological mechanisms for local-global comparisons in visual neurons. *Ann. Rev. Neurosci.* **8**, 407–430 (1985).
- Gilbert, C. D. Circuitry, architecture and functional dynamics of visual cortex. *Cereb. Cortex* **3**, 373–386 (1993).
- Sillito, A. M., Grieve, K. L., Jones, H. E., Cudeiro, J., & Davis, J. Visual cortical mechanisms detecting focal orientation discontinuities. *Nature* **378**, 492–496 (1996).
- Knierim, J. J., & Van Essen, D. C. Neuronal responses to static texture patterns in area V1 of the alert macaque monkey. *J. Neurophysiol.* **67**, 961–980 (1992).
- Kapadia, M. K., Ito, M., Gilbert, C. D., & 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).
- Polat, U., Mizobe, K., Pettet, M. W., Kasamatsu, T., & Norcia, A. M. Collinear stimuli regulate visual responses depending on cell's contrast threshold. *Nature* **391**, 580–584 (1998).
- Gilbert, C. D. & Wiesel, T. N. The influence of contextual stimuli on the orientation selectivity of cells in primary visual cortex of the cat. *Vision Res.* **30**, 1689–1701 (1990).
- Rossi, A. F., Rittenhouse, C. D., & Paradiso, M. The representation of brightness in primary visual cortex. *Science* **273**, 1104–1107 (1996).
- Salin, P. & Bullier, J. Corticocortical connections in the visual system: Structure and function. *Physiol. Rev.* **75**, 107–154 (1995).
- Payne, B. R., Lomber, S. G., Villa, A. E., & Bullier, J. Reversible deactivation of cerebral network components. *Trends Neurosci.* **19**, 535–542 (1996).
- Lamme, V. A. F., Supèr, H., & Spekreijse, H. Feedforward, horizontal, and feedback processing in the visual cortex. *Curr. Opin. Neurobiol.* **8**, 529–535 (1998).
- Hupé, J. M., James, A. C., Payne, B. R., Lomber, S. G., Girard, P., & Bullier, J. Cortical feedback improves discrimination between figure and background by V1, V2 and V3 neurons. *Nature* **394**, 784–787 (1998).
- Schiller, P. H., Malpeli, J. G., & Schein, S. J. Composition of geniculostriate input to superior colliculus of the Rhesus monkey. *J. Neurophysiol.* **42**, 1124–1133 (1979).
- Nothdurft, H. C. Orientation sensitivity and texture segmentation in patterns with different line orientation. *Vision Res.* **25**, 551–560 (1985).
- Desimone, R., & Duncan, J. Neural correlates of selective visual attention. *Ann. Rev. Neurosci.* **18**, 193–222 (1995).
- Vidyasagar, T. R. Gating of neuronal responses in macaque primary visual cortex by an attentional spotlight. *Neuroreport* **9**, 1947–1952 (1998).
- Roelfsema, P. R., Lamme, V. A. F., & Spekreijse, H. Object based attention in primary visual cortex of the macaque monkey. *Nature* **395**, 376–381 (1998).
- Shadlen, M. N., Britten, K. H., Newsome, W. T., & Movshon, J. A. A computational analysis of the relationships between neuronal and behavioural responses to visual motion. *J. Neurosci.* **16**, 1486–1510 (1996).
- Nothdurft, H. C., Gallant, J. L., & Van Essen, D. C. Response modulation by texture surround in primate area V1: correlates of 'popout' under anesthesia. *Vis. Neurosci.* **16**, 15–34 (1999).
- Block, N. How can we find the neural correlate of consciousness. *Trends Neurosci.* **19**, 456–459 (1996).
- Rock, I., Linnett, C. M., Grant, P., & Mack, A. Perception without attention: results of a new method. *Cognit. Psychol.* **24**, 501–534 (1992).
- Pollen, D. A. On the neural correlates of visual perception. *Cereb. Cortex* **9**, 4–19 (1999).
- Bour, L. J., Van Gisbergen, J. A. M., Bruylants, J., & Ottes, F. P. The double magnetic induction method for measuring eye movement - results in monkey and man. *IEEE Trans. BME* **31**, 419–427 (1984).