Dynamics of neuronal sensitivity in visual cortex and local feature discrimination

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A striking aspect of natural scenes is that image features such as line orientation are strongly correlated at neighboring spatial locations but not at distant locations. Thus, during the viewing of a scene, eye movements are often accompanied by a change in the orientation structure of the image. How does this behavior influence the discrimination of local features and their encoding by visual cortical neurons? Here we examined the perceived changes in orientation induced by brief exposure to oriented image patterns in monkeys and humans, and then used reverse correlation to investigate dynamic changes in neuronal sensitivity in the primary visual cortex (V1) of behaving monkeys. Whereas brief adaptation to an oriented grating impaired identification of nearby orientations by broadening orientation selectivity and changing the preferred orientation of individual V1 neurons, it actually enhanced the identification of orthogonal orientations by sharpening neuronal selectivity. Hence, successive exposure to image patches of dissimilar spatial structure enhances both the ability to discriminate local features and the encoding of these features by V1 neurons.

A fundamental issue in the function of the visual cortex is whether its properties are adapted to the statistics of natural stimuli[1–4]. Although visual cortical neurons have a rich repertoire of responses to elementary features of visual stimuli, including contextual and learned features[5–8], exactly how cortical responses relate to environmental statistics is just beginning to be explored quantitatively[4,9–11]. Natural images, despite their complexity, have certain common statistical properties. Simple inspection of a natural scene quickly reveals that neighboring image patches are highly correlated in local features such as orientation, contrast and spatial frequency[9,12–16], whereas distant image patches are poorly correlated (**Fig. 1**). How does the visual system take advantage of this correlational structure of natural images?

While viewing a scene, primates, including humans, make saccadic eye movements several times a second[17–19]. During fixation (between saccades), the portions of a scene that fall within the receptive field of the same V1 neuron are well correlated in local features. Exposure to these spatially correlated image patches induce short-term changes in the steady-state responses of V1 neurons: the response at the preferred orientation is reduced, and hence possibly the correlation among neuronal responses is also reduced[1,20–22]. In theory, brief adaptation to the structure of retinal images could reduce the redundancy of natural signals and improve information transmission[1,4,22]. Adaptation effects have been mainly described, however, by examining how exposure to a certain image pattern affects the subsequent viewing and discrimination of similar patterns. Because distant image patches are structurally uncorrelated and the mean saccade distance during free viewing is relatively large[18,19], fixation at one location is likely to be followed by a saccade to an image patch of largely dissimilar structure (see **Supplementary Fig. 1** online).

How does brief adaptation affect the discrimination of local image patches of dissimilar structure and their encoding by visual cortical neurons? Here we address this question by showing that rapid adaptation affects the signaling capabilities of V1 neurons and perceptual discrimination thresholds. Specifically, we found that brief adaptation to an oriented grating impaired perceptual discrimination of nearby orientations by broadening orientation selectivity and changing the preferred orientation of individual V1 neurons, but it actually enhanced the discrimination of orthogonal orientations by sharpening neuronal selectivity. We suggest that these adaptive changes are used by the visual system to enhance local feature discrimination during natural viewing.

Results

To understand how brief adaptation affects perceptual performance, we devised a delayed match-to-sample task in which subjects (one monkey and two humans) were trained to report whether two circular oblique gratings, briefly flashed for 400 ms, differed in orientation (**Fig. 2a**). To examine how patterned stimuli presented for a duration similar to that of visual fixation affects subsequent orientation identification, the second grating was preceded by a 400-ms adapting stimulus (S_A), which either consisted of a blank patch or was oriented 20° (iso-orientation adaptation) or 90° (orthogonal adaptation) away from the first grating.

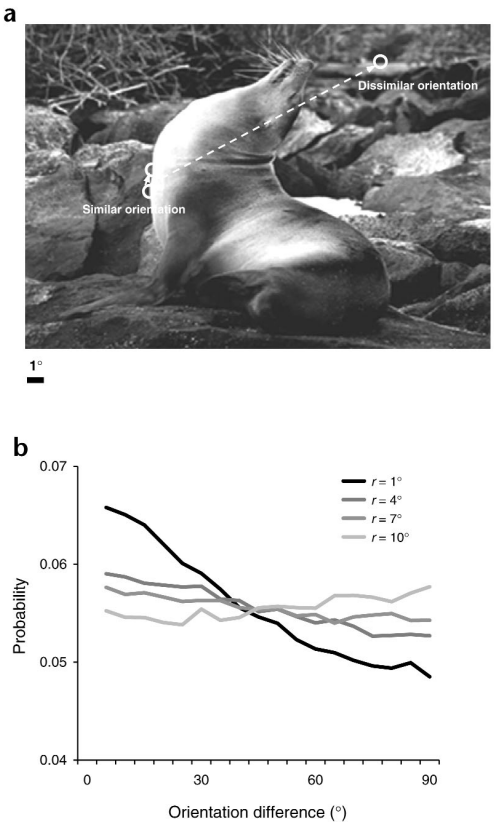

Fig. 1. Correlational structure of natural scenes. We analyzed 40 natural scenes depicting landscapes or animals in their natural environment (images were 640 × 480 pixels and 256 gray levels, and were extracted from a high-resolution, commercial photo-CD library). We determined the orientation of each pixel based on the direction of the local gray-scale gradient in a standard 25-pixel array from the arc tangent of the partial derivative of brightness in a 5 × 5 kernel in the vertical direction, divided by this value in the horizontal direction[11]. Control analyses are described in **Supplementary Note** online. (**a**) Neighboring image patches tend to be highly correlated in spatial structure (for example, orientation), whereas distant patches tend to be only weakly correlated. (**b**) Orientation statistics of natural scenes. After calculating the preferred orientation of each pixel in the image, we determined the probability that pairs of pixels at different distances (r = 1, 4, 7 or 10°) will differ by orientation θ (1° of visual angle was calculated at a viewing distance of 57 cm). We calculated orientation differences for all the pixels in each image (pixels that were weakly tuned, with OSI < 0.1, were excluded from the analysis). Neighboring pixels (for example, r = 1°) have a high probability of having similar orientations, whereas distant pixels (for example, r = 10°) are equally likely to differ by any orientation between 0 and 90°.

We estimated the effect of brief adaptation on perceived orientation by measuring how the tuning curves for two target oblique orientations were altered after iso- and orthogonal adaptation. Contrary to the expectation that orthogonal adaptation would have no effect on performance (but see ref. 23 which reports that 5 s of adaptation facilitates the discrimination of orthogonal gratings), we found that the monkey actually improved when the adapting stimulus was orthogonal to the target (**Fig. 2b** and **c**). After iso-orientation adaptation, however, performance was impaired and the tuning curves broadened and shifted away from the adapting orientation (the test orientations between the adapting and target orientations were judged as tilted away from the adapting stimulus, that is, matched to the target orientation). Monkey and human subjects had significantly altered performance at all adapting orientations in the neighborhood of the target orientation (**Fig. 2d–f**).

Given the brevity of stimulus presentation, our psychophysical results may have been affected by stimulus masking during the presentation of the adapting stimulus. That is, the adapting stimulus might interfere with the stimulus preceding or succeeding it. To control for this possibility, we repeated the adaptation experiments in the two human subjects by replacing the oriented adapting stimulus with an unoriented pattern of similar size consisting of a superposition of eight equally spaced orientations between 0 and 180°. If the observed changes in the profile of orientation tuning curves (**Fig. 2b** and **c**) were due to stimulus masking rather than to orientation-specific adaptation, using an unoriented adapting stimulus should interfere with the short-term memory of the target in a way that affects the shape of the orientation tuning curves. When we used the unoriented adapting stimulus, however, we did not see significant changes in the tuning curve profiles for the two oblique orientations when the tuning curves were compared to those measured during the control condition ($P > 0.1$).

These findings indicate the importance of orthogonal adaptation: the capacity of the visual system to identify orientations improves after brief exposure to a pattern of dissimilar structure. To understand the neuronal correlate of these adaptive changes in perceptual identification, we asked whether V1 neurons also show changes in sensitivity induced by brief adaptation. It is widely thought that adaptation is most effective when the adapting stimulus is close to the neuron's preferred orientation[20,21,24,25], and that adaptation at orientations orthogonal to the neuron's optimal orientation would have little or no effect[21,25]. So far, however, these effects have been examined only with long adaptation times. We reasoned that briefly presented stimuli[20,26] would allow us to examine both the effects of rapid adaptation on cortical responses and the time course of the neuronal events underlying these adaptation effects. These temporal interactions are critical for understanding natural vision, as stimulus statistics at the center of gaze change continuously between eye movements during free viewing (**Supplementary Fig. 1**), thereby inducing temporal dynamics of cortical responses[27].

We described the cortical temporal dynamics after adaptation by estimating the development of orientation tuning using the reverse correlation procedure (refs. 28–30; Felsen, G., Yao, H. & Dan, Y. *Soc. Neurosci. Abstr.* **26**, 408.5, 2000). We thus measured how the orientation tuning of V1 neurons evolves at the millisecond time scale before and after brief adaptation (Dragoi, V., Sharma, J., Miller, E. K. M. & Sur, M. *Soc. Neurosci. Abstr.* **25**, 619.3, 1999). Stimuli consisted of movie sequences in which each frame was a high-contrast sine wave grating of pseudorandom orientation, which was synchronized with the refresh of the monitor and flashed at 60 Hz. The orientation domain was sampled in steps of 11.25°, and each orientation was presented seven times during each movie strip. Monkeys were trained to hold fixation within a small 0.5° window while the movies were presented in the center of the receptive field of individual V1 neurons recorded in the foveal and parafoveal representation (**Fig. 3a**). Each trial consisted of presentations of control stimuli (movie strips alone) or adaptation stimuli in which each movie was preceded by a 400-ms sine wave drifting grating of fixed orientation. At the end of each adap-

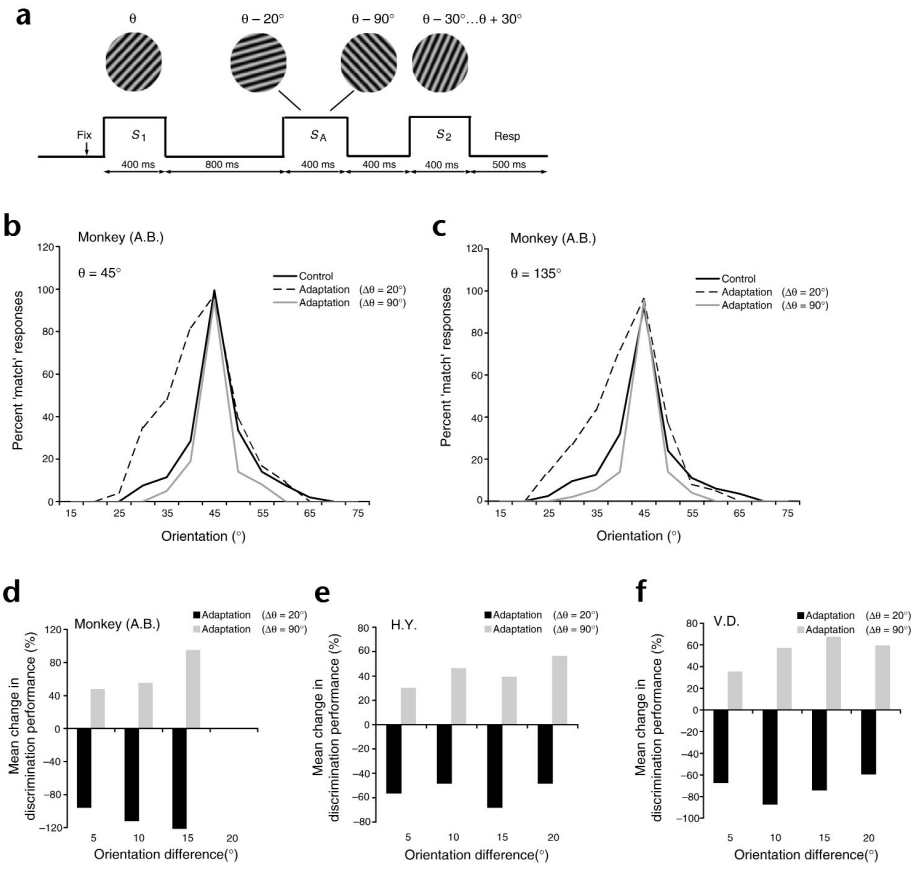

Fig. 2. Psychophysics of orientation discrimination after brief adaptation. (**a**) Stimulus configuration. S_1, target stimulus with orientation θ; S_A, adapting stimulus with orientation θ – 20°, θ – 90° or blank; S_2, test stimulus with orientation θ ± 30° (step 5°). (**b**, **c**) Monkey orientation tuning curves obtained during control condition (solid black line) and after iso-orientation (dashed line) or orthogonal (gray line) adaptation for the two target oblique orientations. The *y* axis represents the percentage of responses for each test orientation when the subject (A.B.) judged that the test orientation matched that of the target ('match' responses). The *x* axis represents the test orientations. (**d**–**f**) Mean change in discrimination performance after iso-orientation and orthogonal adaptation. After calculating orientation tuning curves during both control and adaptation conditions for each subject, changes in discrimination performance were evaluated for test orientations tilted ±5°, ±10°, ±15° and ±20° away from the target by calculating the percentage change in 'match' responses after iso-orientation (black bars) and orthogonal (gray bars) adaptation relative to the control condition. The *y* axis represents the mean change in discrimination performance obtained after averaging data on test orientations that were symmetrical with respect to the target. Data is from one monkey (A.B.) and two human subjects (H.Y. and V.D.).

tation session, we conducted recovery experiments in which the control stimulation was repeated for a similar number of trials as during the pre-adaptation condition. For each recorded action potential, we determined which orientation had been presented at various preceding times in the movie sequence. Spikes from completed trials were accumulated in a two-dimensional array based on stimulus orientation and time delay before spiking. We obtained a mean spike count for each stimulus orientation by dividing each spike counter by the number of rewarded trials and by the number of stimulus repetitions within each trial.

Brief exposure to an adapting orientation induced changes in the dynamics of orientation tuning. For a representative neuron that was successively adapted to two different orientations located on opposite flanks of the tuning curve around its preferred orientation (cell 1 in **Fig. 3b**), orientation tuning developed with a peak at 102.5° after a delay of 56 ms. Then, in the next 16 ms, tuning gradually sharpened ($P < 0.001$, comparing the trial-by-trial variability in preferred orientation between control and adaptation conditions). At large time delays (>104 ms), the orientation tuning curve was relatively flat (because cells can only respond with a finite number of spikes to a flashed stimulus). Exposure to an adapting orientation altered the dynamics of orientation tuning (**Fig. 3b**, middle column): the orientation preference peaked first at the pre-adaptation value with a delay of 56 ms. During the next 8 ms, the cell's selectivity broadened on the flank toward the adapting orientation ($P < 0.001$), and a new preferred orientation emerged in a direction away from the adapting stimulus. This new preferred orientation became sharper within the next 8 ms ($P < 0.001$). Cell 1 showed another repulsive shift in preferred orientation when the adapting stimulus was presented on the opposite flank of the tuning curve, confirming these dynamics of adaptation (**Fig. 3b**).

These results suggest an active and nonlinear reorganization of V1 response selectivity by the temporal context of stimulation, which acts on a millisecond time scale. To understand how this reorganization affects the full set of orientations, we investigated the rela-

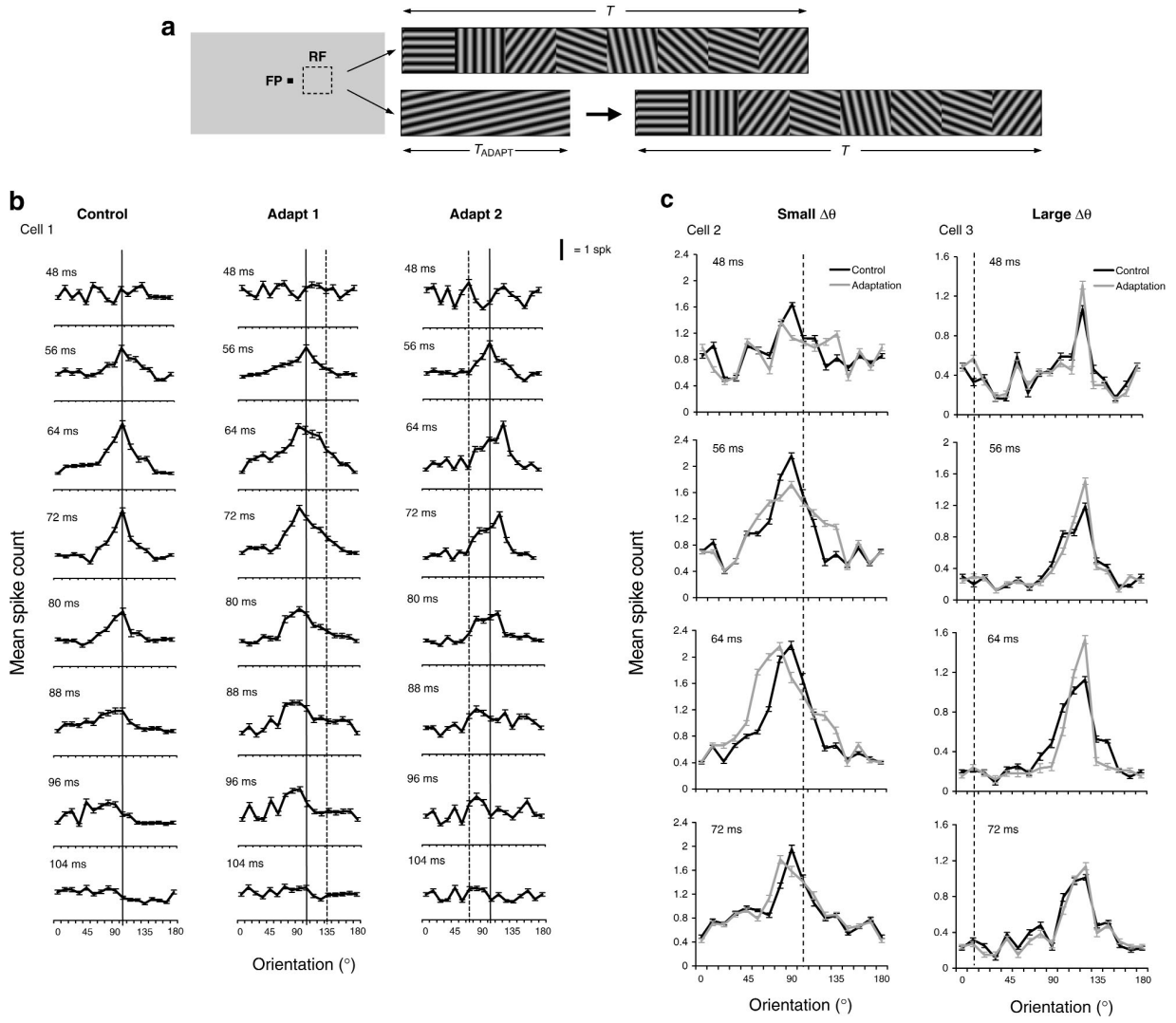

Fig. 3. Temporal dynamics of brief adaptation in V1 neurons. (**a**) Schematic representation of the stimulus sequence. Animals fixated centrally (FP) while stimuli were presented in the receptive field center (RF). Two types of trials were used: movie strips presented for *T* ms each (control, 112 frames at 60 Hz) or movie strips preceded by a drifting grating of fixed orientation presented for T_{ADAPT} = 400 ms (adaptation condition). (**b**) Temporal dynamics of orientation tuning of one representative cell (cell 1) that was successively adapted to two different orientations. The graphs within each column show the development of orientation tuning at different temporal delays during three conditions: control (left), adaptation to the first orientation (middle), and adaptation to the second orientation (right). The solid line marks the control preferred orientation, whereas the dashed line marks the orientation at which adaptation was performed in each condition. (**c**) Changes in the time course of orientation tuning dynamics. Adaptation near the cell's preferred orientation delays the development of orientation tuning (cell 2, left column), whereas adaptation at an orthogonal orientation relative to the cell's optimal orientation accelerates the development of orientation tuning (cell 3, right column). The graphs within each column show the development of orientation tuning for two neurons at different temporal delays during control (black) and adaptation (gray) conditions. The adapting orientation is marked by the dashed line. Error bars represent s.e.m.

tionship between the dynamics of brief adaptation and the relative orientation difference between the cell's optimal orientation and that of the adapting stimulus (Δθ). Brief adaptation near a cell's preferred orientation (small Δθ) delayed the development of orientation selectivity (**Fig. 3c**, cell 2), whereas adaptation orthogonal to the cell's preferred orientation (large Δθ) accelerated the development of orientation selectivity (**Fig. 3c**, cell 3). Indeed, cell 2 showed a pronounced increase in orientation tuning bandwidth after adaptation (latencies 56 and 64 ms, $P < 0.001$), along with an early decrease in mean spike count and a change in preferred orientation. In contrast, after adaptation to an orthogonal orientation, cell 3 showed a sharpening in orientation tuning at virtually every latency ($P < 0.01$), along with an increase in responsiveness, but the preferred orientation of this neuron remained unchanged ($P > 0.1$).

To examine the generality of the temporal interactions associated with rapid cortical adaptation, we characterized the dynamics of orientation tuning induced by brief adaptation in a population of V1 neurons ($n = 86$) and calculated, for each time delay, the statistical significance (Student's *t*-test) of the change in preferred orientation and strength of tuning

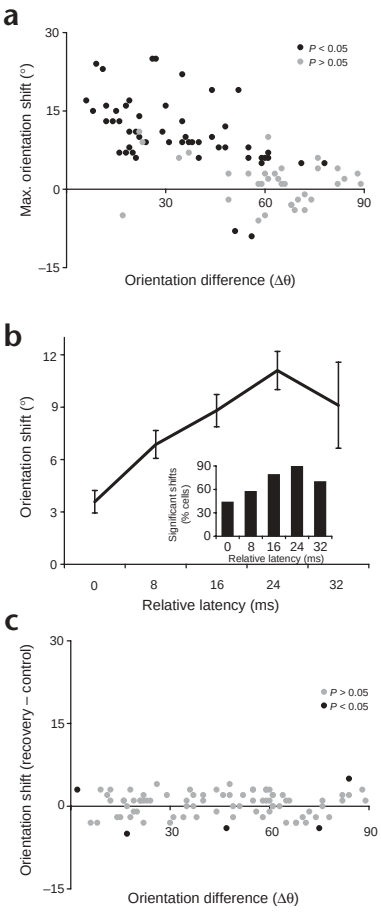

Fig. 4. Population analysis of adaptation-induced dynamics of orientation preference. (**a**) The maximum post-adaptation shift in preferred orientation as a function of the difference between the cell's preferred orientation and that of the adapting stimulus (n = 86 cells). Positive numbers indicate repulsive shifts; negative numbers indicate attractive shifts (with respect to the adapting orientation). Cells that show significant shifts in preferred orientation based on a trial-by-trial comparison between adaptation and control conditions are shown in black ($P < 0.05$); those that do not show significant shifts are shown in gray ($P > 0.05$). (**b**) The mean post-adaptation shift in preferred orientation (n = 52 cells) measured at different time delays between the spike train and the onset of the movie sequence. Relative latency was calculated with respect to the time when the first tuned response was observed (OSI > 0.1). Inset, relative latency of orientation shifts after adaptation (n = 52 cells). These are the cells that showed significant orientation shifts after adaptation (filled circles in **Fig. 4a**). (**c**) Maximum orientation shifts after recovery (n = 86 cells). The difference between the maximum recovery and the control preferred orientation (y axis) is shown as a function of the difference between the cell's preferred orientation and that of the adapting stimulus (x axis). Cells that showed significant shifts in preferred orientation based on a trial-by-trial comparison between control and recovery conditions are shown in black ($P < 0.05$); those that did not show significant shifts are shown in gray ($P > 0.05$).

(Methods). For most neurons, 400 ms of adaptation near the optimal orientation induced repulsive shifts in orientation preference. We also calculated the maximum orientation shift (at any latency) as a function of Δθ (**Fig. 4a**). Consistent with previous results obtained in V1 of anesthetized cats[21,31], the maximum orientation shift magnitude was largest for small Δθs, and the shifts become nonsignificant as Δθ approached 90° (Pearson's correlation coefficient, $r = –0.646$, $P < 0.00001$). **Fig. 4b** examines the dynamics of the shift in preferred orientation after brief adaptation. When orientation tuning emerged for the first time (0 ms relative latency, calculated with respect to the time delay of the first tuned response, OSI > 0.1), the difference between the control and adaptation-induced optimal orientation was small. As time delay increased (larger relative latencies), the shift magnitude also increased until almost 90% of neurons showed significant orientation shifts ($P < 0.05$) for relative latencies of 24 ms (**Fig. 4b**, inset), after which the shift magnitude decreased until orientation tuning disappeared at larger time delays. Orientation preference returned to the original (control) optimal orientation during the recovery condition ($P > 0.05$, **Fig. 4c**). On the basis of these data, we suggest that local feedback is likely to be involved in shaping visual cortical responses. After brief adaption, the initial orientation preference (at the preadaptation preferred orientation) observed immediately after orientation selectivity emerges, could be due to feedforward mechanisms[34–36]. Subsequently, delayed intracortical feedback[35,36] due to local V1 circuits or to inputs from cortical areas other than V1, in combination with intracortical inhibition[37–39], could shift the preferred orientation repulsively with respect to the adapting orientation.

We related the adaptation-induced changes in the strength of orientation tuning of neurons to the changes in perceptual performance by calculating how the orientation selectivity index (OSI; see Methods) evolves in time before and after adaptation (**Fig. 5a**). There was a significant correlation between the maximum change in OSI (difference between peak control and postadaptation OSI regardless of latency) and Δθ ($r = 0.759$, $P < 0.00001$), suggesting that brief adaptation reduces or facilitates orientation tuning depending on whether Δθ is small (< 60°) or large (> 60°). To understand how adaptation changes the time course of orientation tuning at each time frame, we divided our population of cells into two subpopulations depending on the Δθ values (**Fig. 5b**). There was an overall reduction in the strength of orientation selectivity when Δθ < 60° ($P < 0.01$), and a delayed enhancement of orientation selectivity when the adapting stimulus was nearly orthogonal to the cell's preferred orientation ($P < 0.01$, relative latencies longer than 8 ms). These changes in the strength of orientation tuning after adaptation are compatible with changes in the absolute latency of orientation tuning, that is, the time delay at which the first tuned response was seen: iso-orientation adaptation delayed the development of orientation selectivity, whereas cross-orientation adaptation accelerated the development of orientation-selective responses (**Supplementary Fig. 2**). After adaptation, the strength of orientation selectivity for the population of neurons recovered to the initial (control) values (**Fig. 5c**, $P > 0.05$).

Given the time constraints of the reverse correlation experiments in awake animals (approximately 3–4 hours for the control, adaptation and recovery protocol), each cell in **Figs. 4** and **5** was tested with only two adapting stimuli per recording. It is thus possible, in theory, that we inadvertently used larger orientation differences between adapting and preferred orientation for those cells that were more broadly tuned. In this case, **Fig. 5a** could possibly reflect a relationship between orientation bandwidth and adaptation (poorly tuned cells would show weaker adaptation effects), rather than a relationship between changes in orientation preference and the orientation differ-

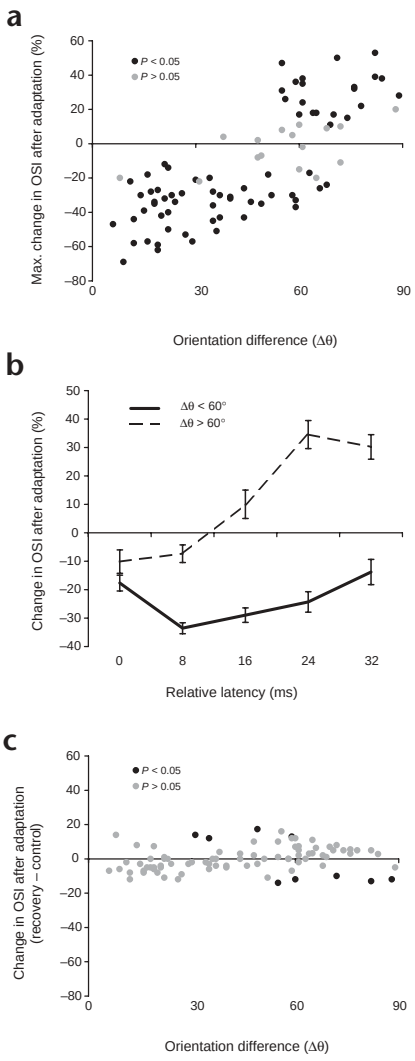

Fig. 5. Population analysis of adaptation-induced dynamics of orientation selectivity. (**a**) Maximum change in OSI after adaptation, as a function of Δθ (n = 86 cells). Cells that showed changes in OSI based on a trial-by-trial comparison between adaptation and control conditions are shown in black ($P < 0.05$); those that did not show significant changes are shown in gray ($P > 0.05$). (**b**) The mean change in OSI after adaptation at different relative latencies, for Δθ < 60° (solid line) and Δθ > 60° (dashed line). All changes are calculated with respect to the control OSI values at the same relative latency. Error bars represent s.e.m. (**c**) The maximum change in OSI after recovery (n = 86 cells). The difference between the maximum recovery and the control OSI plotted against the difference between the cell's preferred orientation and that of the adapting stimulus. Cells that showed significant changes in OSI based on a trial-by-trial comparison between control and recovery conditions are shown in black ($P < 0.05$); those that did not are shown in gray ($P > 0.05$).

ence between the adapting and preferred orientation. To control for this, we examined the relationship between OSI and Δθ for the neurons in our population, and did not find a significant correlation ($r = 0.06$, $P > 0.1$).

Collectively, our results led us to ask what significance the observed adaptation-induced temporal dynamics of cortical responses have for vision. We thus examined whether and how brief adaptation alters orientation discrimination by individual neurons. As the changes in orientation tuning that we reported in **Fig. 5** were measured using a global estimate of tuning strength, such as the OSI, which is based on responses to a broad range of orientations, it is possible that OSI may not necessarily be the appropriate measure for capturing a neuron's sensitivity to small orientation differences. We thus estimated a neuron's ability to discriminate gratings oriented 11.25° from its peak orientation by calculating the mean sensitivity (d')[40] at the peak orientation response, before and after adaptation to a range of Δθ values. Adaptation reliably improved orientation discrimination of the population of neurons (**Fig. 6a**, points that lie above the diagonal; $P < 0.00002$). The change in orientation discrimination after adaptation was closely related to Δθ (**Fig. 6b**). Thus, adaptation near the cell's preferred orientation improved discrimination performance only weakly (for example, Δθ < 22.5°, $P > 0.1$), whereas performance improved almost twofold when adapting stimuli were orthogonal to the cell's preferred orientation (Δθ > 67.5°, $P < 0.01$, Pearson test). Paralleling the changes in OSI (**Fig. 5**), this improvement in discrimination performance after orthogonal adaptation (Δθ > 45°) developed gradually in time and reached a peak at 24 ms relative latency ($P < 0.01$, **Fig. 6c**). In contrast, we found that iso-orientation adaptation (Δθ < 45°) impaired the neurons' discrimination performance shortly after orientation tuning emerged ($P < 0.01$), and then mildly improved discrimination at large relative latencies.

In sum, we found pronounced orientation-dependent effects: adaptation away from a cell's optimal orientation preserves preferred orientation but strengthens orientation tuning and increases discrimination performance, whereas adaptation near the cell's optimal orientation induces a repulsive shift in preferred orientation along with an increase in tuning bandwidth and a mild increase in orientation discrimination performance. A potential problem with using the absolute orientation difference between a cell's preferred orientation and that of the adapting stimulus (Δθ) is that this measure is insensitive to the bandwidth of the neuron. Thus, an adapting stimulus with a relatively small Δθ may be 'distant' in orientation for a neuron that has a narrow orientation bandwidth, but 'nearby' for a neuron with a broad bandwidth. To control for this, we normalized the adaptation orientation difference by the strength of orientation tuning, and calculated for each cell the relative orientation difference as $\Delta\theta' = \Delta\theta[(OSI - OSI_{min})/(OSI_{max} - OSI_{min})]$, where OSI_{min} and OSI_{max} are the minimum and maximum OSI across the population. Replotting our variables against Δθ′, however, did not alter our results (**Supplementary Fig. 3**). Indeed, we found a significant negative correlation between the orientation shift magnitude and Δθ′ ($r = -0.404$, $P < 0.001$), a significant positive correlation between the maximum change in OSI after adaptation and Δθ′ ($r = 0.62$, $P < 0.00001$) and an improvement in orientation discrimination after a large Δθ′.

Discussion

The changes in orientation-selective responses of awake monkey V1 neurons reported here demonstrate the temporal dynamics of brief adaptation on the time scale of visual fixation. Adaptation alters a broad range of responses with different time courses: after iso-orientation adaptation, cortical responses develop initially at the control preferred orientation and then shift away by broadening their selectivity. In contrast, orthogonal adaptation preserves the optimal orientation and improves neuronal selectivity. Previous adaptation studies[20,21] have characterized

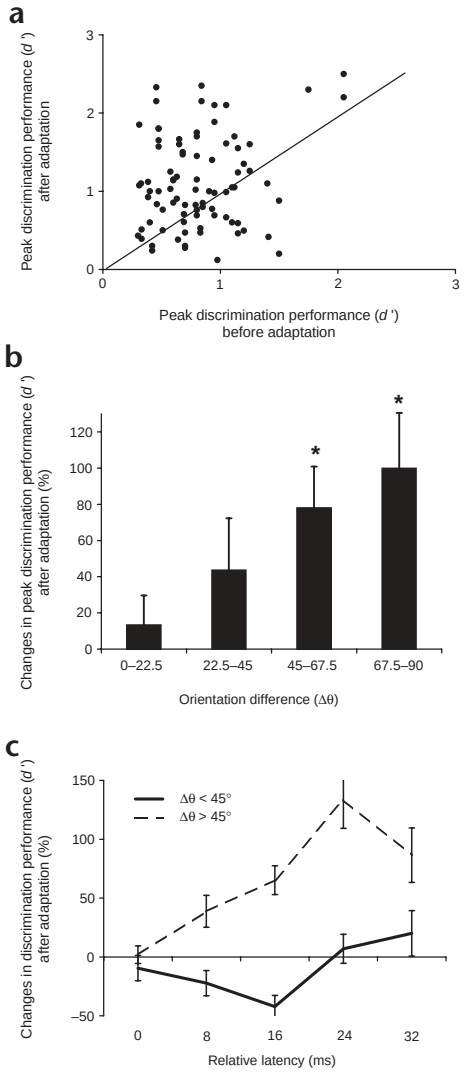

Fig. 6. Changes in orientation discrimination performance after adaptation. (**a**) Change in the discriminability (d') of two gratings differing in orientation by 11.25°, after adaptation to a range of orientations. For each neuron (filled circle), we plotted the mean d' calculated at the time delay for which orientation tuning was sharpest. Cells showing improvement in discriminability are situated above the diagonal. (**b**) Change in orientation discrimination (d') after adaptation as a function of $\Delta\theta$. Each bar represents the mean change in discriminability for neurons pooled in different $\Delta\theta$ intervals shown on the *x* axis. Asterisks denote statistical significance ($P < 0.01$) from pre-adaptation values. (**c**) Dynamics of discrimination performance (d') after adaptation. Changes in discrimination are calculated at each latency relative to the onset of orientation tuning. Error bars represent s.e.m.

the 'steady-state' changes in cortical responses after brief exposure to a fixed orientation, but the temporal dynamics leading to these changes have remained unknown.

Whereas a number of competing mechanisms—slow-hyperpolarizing Ca^{2+}-activated and Na^{+}-activated potassium channels[41], depression of feedforward excitatory synapses[42,43] or disinhibitory intracortical interactions[21,37]—have been proposed to explain steady-state effects of adaptation, dynamic changes in response selectivity have not yet been addressed. We suggest that most of the changes reported here are likely to be explained by network mechanisms that act at different times. Adaptation is postulated to reduce neuronal responses at the adapting orientation. Brief adaptation near a cell's preferred orientation could cause a reduction in recurrent excitation and a change in the gain of local recurrent circuits that could generate, after a small delay, a broadening in orientation tuning along with a shift in optimal orientation away from the adapting orientation. In contrast, adaptation orthogonal to the cell's preferred orientation could engage multiple short-term plasticity mechanisms that could induce asymmetric changes in synaptic efficacy at excitatory and inhibitory synapses[44,45] to cause a sharpening of orientation tuning without a change in optimal orientation.

Adaptation effects in perception and in cortical neurons have been described before, but the way in which they are related to natural signal statistics has not been investigated. We have examined the relationship between adaptation and the correlational structure of natural scenes (the fact that image patches are highly correlated in local features at small spatial separations, and that the strength of correlation decreases as the distance between patches increases). Describing this relationship is central to understanding rapid temporal interactions during natural vision, particularly the effect of successive fixations during viewing. Indeed, because the mean saccade distance during free viewing is relatively large, successive fixations are likely to be made on image patches of dissimilar structure. We have shown that, depending on the spatial structure of the image patch which fell on the retina during the previous fixation, brief adaptation on the time scale of visual fixation alters the time course of orientation-selective responses. Specifically, successive exposures to image patches of dissimilar structure enhance both the capacity of the visual system to identify orientations and the neuronal performance in V1. Given the ubiquity of successive saccades to images of dissimilar structure during natural vision, our data suggest that the visual system has adapted to the correlational structure of images so as to encode local features more efficiently.

Methods

Electrophysiology. Single-neuron recordings were made from two awake, behaving macaque monkeys (*Macaca mulatta*) with extracellular electrodes lowered transdurally. Details of recordings[21] and surgical procedures[46] are given elsewhere. All experiments were performed under protocols that were approved by MIT's Animal Care and Use Committee and conformed to NIH guidelines. Eye position was continuously monitored using an infrared eye tracking system (Iscan, Burlington, Massachussetts). Monkeys were trained to fixate on a small spot (0.1°) presented on a video monitor placed at a distance of 57 cm from the monkey's eye. Once the animal achieved stable fixation for 100 ms, the visual stimulus was presented within the neuron's receptive field. Receptive fields were located within 2.5° of the center of fixation. The monkeys were required to maintain fixation throughout the stimulus presentation to earn a juice reward; the trial was automatically aborted if fixation instability exceeded 0.25° at any time during stimulus presentation. Stimuli were movie strips in which each frame consisted of a 5 × 5° sine-wave grating of 2 cpd spatial frequency and 75% contrast, presented binocularly. Each movie strip was presented for ~1.86 s (16 orientations × 7 repeats × 60 Hz). The stimulus spatial phase was randomized across frames for each orientation. Control and adaptation trials were grouped in blocks of 400–500 trials, two repeats each. The reverse correlation calculation was averaged over the entire movie duration during control, adaptation and recovery conditions (eliminating the onset response to the movie sequence—the first 200–400 ms—did not alter our results significantly). To increase the effectiveness of adaptation, we used drifting sine-wave gratings (temporal frequency 3 Hz; similar spatial characteristics

as the flashed gratings) as adapting stimuli because we found that drifting gratings evoke stronger responses than flashed stimuli. To examine whether our results are affected by differences in the quality of fixation between control and adaptation conditions, we calculated the deviation of eye position along the vertical and horizontal axes during the movie sequence presentation. The average standard deviation of the *x*- and *y*-position of the eye was 0.039° and 0.045° (control), and 0.044° and 0.041° (adaptation). These values were not statistically different ($P > 0.1$). Statistical significance was established with the Student's *t*-test (or Pearson test for correlations) unless otherwise stated.

For each neuron, we determined the preferred orientation and the OSI, which measures the strength of orientation tuning, every 8 ms, as described previously[45]. The Fourier components were extracted from the orientation tuning curve and then normalized by dividing by the mean spike count of the cell during stimulus presentation: $a = \sum_{i=0}^{n-1} R(\theta_i)\cos(2\theta_i)$; $b = \sum_{i=0}^{n-1} R(\theta_i)\sin(2\theta_i)$, where responses, $R(\theta_i)$, represent the mean spike count obtained for the set of $n = 16$ orientations θ_i $\{i = 0, 1, \ldots n-1\}$ which are uniformly distributed over 0–180°. Preferred orientation, θ, was calculated as $\theta = 0.5\arctan(b/a)$ if $a > 0$ or $\theta = 90 + 0.5\arctan(b/a)$ if $a < 0$. If $a > 0$ and $b < 0$, $\theta = 180 + 0.5\arctan(b/a)$. The strength of orientation tuning was given by OSI = c/M, where $c = \sqrt{(a^2 + b^2)}$, and M is the mean spike count[47]. At the end of each adaptation session, we repeated the movie sequences that were used to estimate orientation selectivity during the control condition. We included in the analysis only those cells that showed statistically significant recovery from adaptation for both preferred orientation and tuning strength measurements (**Figs. 4c** and **5c**). To further verify the accuracy of orientation preference measurements using the reverse correlation technique, at the end of each experiment we used sine-wave drifting gratings which were randomly presented for 1,500 ms at eight orientations between 0–180° and two opposite directions of motion to directly measure the steady-state preferred orientation. To determine orientation discrimination performance, we calculated d' before and after adaptation for each time delay between the spike train and the movie sequence as $d' = [(R_1 - R_2)/(\sqrt{\{(SD_1^2 + SD_2^2)/2\}}$ (difference between the mean spike rates at two adjacent orientations divided by the r.m.s. standard deviation)[40]. For each neuron, we averaged the two d' values corresponding to the orientations symmetric with respect to the peak response orientation.

Psychophysics. Psychophysical data was obtained from one macaque monkey and two human subjects (H.Y. and V.D.; both gave informed written consent to participate). (i) Monkey psychophysics. We trained one monkey in a delayed-match-to-sample orientation identification task (the same monkey provided the majority of the physiological data). Stimuli were presented binocularly on a computer screen at a viewing distance of 57 cm, and consisted of 75% contrast 2 cpd sinusoidal circular gratings (5° in diameter) presented in the center of fixation (a red fixation point of size 0.1° always remained on the center of the screen). Each trial consisted of a 3-s cycle. The monkey triggered the trial by holding the bar, and after 100 ms of fixation, stimuli were flashed in the center of fixation: the target was flashed for 400 ms at an oblique orientation, θ = 45° or 135°, followed after 800 ms by an adapting stimulus flashed for 400 ms. The adapting stimulus consisted of a blank screen (uniform gray, 35 cd m^{-2}) or a sinusoidal grating (75% contrast, orientation θ − 20° or θ − 90°). After a brief delay of 400 ms after the offset of the adapting stimulus, a test grating (75% contrast, orientation range θ ± 30°, random presentations at 5° orientation resolution) was briefly flashed for 400 ms. Although introducing a delay between the adapting and test stimuli tends to reduce the effects of adaptation, we finally had to settle for a relatively large delay (400 ms) to ensure an identification performance of at least 85% at the 'match' orientation. At the end of stimulus presentation, the monkey was required to release the bar within 500 ms when the test orientation matched that of the target. The next trial started after an intertrial interval of 5 s. Data collection took place only after the completion of a 50-day practice period at the end of which orientation identification performance had stabilized. After calculating orientation tuning curves during both control and adaptation conditions, the changes in preferred orientation and the strength of tuning (OSI) were determined using the same method as that used for V1 neurons. (ii) Human psychophysics. The task was similar to the monkey orientation identification, with two exceptions: eye movements were not monitored and responses were recorded as key presses.

Note: Supplementary information is available on the Nature Neuroscience website.

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Competing interests statement

The authors declare that they have no competing financial interests.

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