

Response Plasticity in Primary Visual Cortex and its Role in Vision and Visuomotor Behaviour: Bottom-up and Top-down Influences

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Neurons in the primary visual cortex (V1) have been traditionally considered to respond exclusively and steadily to the physical properties of visual stimuli presented within their receptive fields. Indeed, since V1 neurons are mainly involved in processing elementary features of visual stimuli such as orientation or direction of motion, they were long believed to possess stable or unchanging properties. However, another view has emerged in the past 15 years. According to this view, V1 responses are strongly influenced by the history of visual stimulation. Such response changes can be driven by properties of previously viewed visual stimuli (bottomup changes), or by aspects of internal state, including an internal representation of previous stimuli (top-down changes). In effect, the temporal content of visual stimulation results in short term experience-dependent plasticity in local as well as distributed cortical circuits, and these changes are manifest as changes in neuronal responses, visual perception and visuomotor behavior. In this review, we describe our recent findings demonstrating rapid plasticity of responses in V1 neurons resulting from time-dependent bottom-up and top-down influences.

Indexing terms: xxxx

A classic example of short-term bottom-up plasticity in V1 is offered by the phenomenon of pattern adaptation, by which selective exposure for a short time to patterned stimulation induces transient changes in the selectivity of V1 neurons. Pattern adaptation has been characterized with respect to many stimulus dimensions, such as orientation [1-6] contrast [4, 7-9], spatial frequency [7,10], direction of motion [2, 11-12], and velocity [2]. A prominent form of pattern adaptation in the visual cortex is orientation adaptation. This phenomenon can be simply demonstrated by an instant perceptual experiment. If we stare for a brief period of time at oblique lines, the perceived orientation of vertical lines appears tilted away from the obliques; this is the well-known tilt aftereffect [13-15]. This suggests that visual experience could alter the functional properties of individual neurons and of local networks in the early visual cortex of the adult brain. Importantly, rapid plasticity during the viewing of natural scenes seems to directly influence visual networks and ongoing vision.

An interesting top-down influence on V1 responses has recently been shown to involve an internal construct of stimulus location: the temporal order and hence the statistics of stimulus appearance at a particular location has a strong influence on neuronal responses and on visuomotor behavior [16]. That is, neurons even in early visual cortex are part of a distributed network that computes

stimulus probability and uses it to move the eyes or make other movements.

BOTTOM-UP PLASTICITY: THE INFLUENCE OF PATTERN ADAPTATION ON ORIENTATION-SELECTIVE RESPONSES IN V1

Our knowledge about adaptation in early visual cortex comes from studies demonstrating that exposure to a potent stimulus for several minutes can cause a reduction in sensitivity to stimulus attributes such as contrast or spatial frequency [1,3-4,7-8]. In the light of these experiments, cortical adaptation has been viewed for many years as a local phenomenon mediated by depression of firing at the level of individual neurons, possibly involving tonic hyperpolarization of the membrane potential of V1 cells [9] due to synaptic depression [17-18] or to a slow hyperpolarizing membrane potassium current [19].

However, in a recent study [6], we studied adaptation-induced orientation plasticity in V1, and found, in contrast to previous results, that adaptation causes both depression and enhancement of responses to a range of stimulus orientations along with the reorganization of the entire profile of the orientation tuning curve. For example, Fig 1a shows how the preferred orientation of one representative V1 cell changes after 2 mins of exposure to one orientation located on one flank of the cell's tuning curve, followed by a period of recovery, subsequent adaptation to a different orientation located on the opposite flank with respect to the

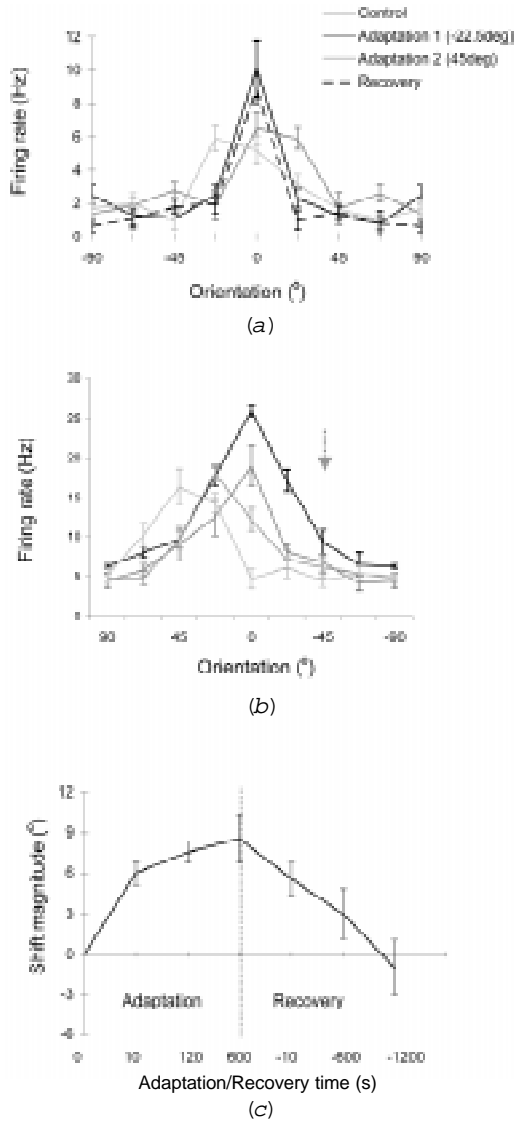


Fig 1 Adaptation-induced orientation plasticity (a) Orientation tuning curves of one representative V1 neuron that was successively adapted to 2 different orientations. Each graph represents orientation tuning during four conditions: control (black), adaptation to the first orientation (dark gray), adaptation to the second orientation (light gray), and recovery (black, dashed line). In this tuning curve display convention, the control optimal orientation is represented as 0°, and all subsequent tuning curves (during adaptation and recovery) are represented relative to the control condition (b) Tuning curves of neurons that show adaptation-induced response suppression on the near flank and response facilitation on the far flank. Each cell was serially exposed to different adaptation periods: 10-s, 2 mins, and 10 mins. Tuning curves were calculated in each of the four conditions: control (black), 10-s adaptation (dark gray), 2-min adaptation (medium gray), and 10-min adaptation (light gray). The adapting orientation is marked by the gray arrow (c) Time course of adaptation and recovery. The graph shows the mean shift magnitude \pm S.E.M. as a function of adaptation and recovery time for a subpopulation of 7 neurons. The orientation shift magnitude was calculated after adaptation to a stimulus presented for 10 s, 2 mins, and 10 mins, followed by recovery to a blank stimulus presented for 10 s, 10 mins, and 20 mins

preferred orientation, and a final period of recovery. When the difference between the cell's preferred orientation and that of the adapting stimulus ($\Delta\theta$) is -22.5° , there is a shift in preferred orientation to the right, away from the adapting stimulus. In contrast, when the adapting stimulus is presented on the right flank of the tuning curve ($\Delta\theta = 45^\circ$), the preferred orientation shifts to the left and then returns to the original value after 10 mins of recovery.

These effects of orientation adaptation are short-term: the shift in preferred orientation increases with adaptation time until it asymptotes at about 10 mins of adaptation, and then reverses to the original level when the adapting stimulus is removed. Figure 1b shows the behavior of one cell that exhibits significant shifts in orientation following adaptation to a stimulus oriented 45° away from the cell's peak orientation [6]. Both the response reduction on the near flank and facilitation on the far flank build up gradually in time: increasing the adaptation time from 10 s to 10 mins shows a progressive depression of responses on the near flank and a progressive facilitation of responses on the far flank. Interestingly, adaptation and recovery develop at two different time scales, with the rate of recovery being at least an order of magnitude slower than the rate of adaptation (Fig 1c).

Rapid adaptation-induced plasticity

An important question about orientation plasticity is whether the different forms of response change have adaptive significance for vision. Whereas long-term cortical plasticity has been used to explain certain kinds of perceptual learning, the functional implications of the more rapid forms of plasticity have been less clear. For instance, plasticity induced by short-term adaptation to oriented contours is considered to underlie the tilt aftereffect, but the tilt aftereffect leads to a misperception of contour orientation and thus it may be a maladaptive or negative effect. The positive effects of orientation adaptation have been less clear.

Next we asked whether cortical plasticity is involved during the rapid processing of image patterns during natural viewing [20]. During the viewing of a natural scene, we make saccadic eye movements several times a second [21-22]. Between successive saccades, during visual fixation, the portions of a scene that fall within the receptive fields of V1 neurons are well correlated in local features. Brief adaptation during exposure to such spatially correlated image patches is known to induce short-term changes in the response of V1 neurons, by reducing the response at the preferred orientation and hence possibly the correlation among neuronal responses [23-24]. However, adaptation effects have been mainly described by examining how exposure to a certain image pattern affects the subsequent viewing and discrimination of similar patterns, thus ignoring the properties of natural viewing. Indeed, during natural vision we often make large saccades

to explore new regions of visual space, with local attributes (*e.g.*, orientation) that are typically uncorrelated to the previous fixation (Fig 2). Therefore, fixation at one location is likely to be followed by a saccade to an image patch of dissimilar structure. How does brief adaptation affect the discrimination of local image patches of dissimilar structure and their encoding by visual cortical neurons?

We have shown that orientation discrimination by humans and monkeys is markedly improved when an adapting grating is presented briefly, for a few hundred msec (on the time scale of visual fixation), followed by a test grating that is orthogonal in orientation to the adapting grating. Rapid adaptation also affects the signaling capabilities of V1 neurons. Specifically, while brief adaptation to an oriented grating broadens orientation selectivity and changes the preferred orientation of individual V1 neurons, it actually enhances the discrimination of orthogonal orientations by sharpening neuronal selectivity.

While most work on adaptation effects on neuronal responses has employed long adaptation and stimulus-response times, stimuli which are presented briefly [3,5] are necessary for examining both the effects of rapid adaptation on cortical responses and the temporal development of neuronal interactions underlying adaptation effects. These temporal interactions are critical for providing clues to the role of temporal interactions in natural vision, as the changing stimulus statistics between eye movements during free viewing introduces complex dynamics in cortical responses.

One efficient way to capture the dynamics of neuronal responses after adaptation would be to estimate the development of orientation tuning by implementing the



Fig 2 Image statistics during natural vision. While viewing a scene, a short saccade is likely to land on an image patch of similar orientation structure, whereas a long saccade is likely to land on an image patch of dissimilar orientation structure

reverse correlation procedure [25-27]. We thus measured how the orientation tuning of V1 neurons evolves at the millisecond time scale before and after brief adaptation. We stimulated V1 neurons of awake monkeys with movie sequences in which each frame was a high-contrast sine-wave grating of pseudorandom orientation synchronized with the refresh of the monitor and flashed at 60 Hz. The orientation domain was sampled in steps of 11.25 deg, and each orientation was presented 7 times during each movie strip. Spikes were recorded during a control condition (in which movie strips were presented alone) or immediately after adaptation (in which movie strips were preceded by a 400-ms sine wave drifting grating of fixed orientation). For each recorded action potential, the orientation that had been presented at various preceding times in the movie sequence was determined. Spikes from completed trials were accumulated in a two-dimensional array based on stimulus orientation and time delay before spiking. A mean spike count was obtained 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.

Figure 3 shows two examples of cells with distinct behaviors during brief adaptation. When the adapting stimulus orientation is near a cell's preferred orientation (small $\Delta\theta$), the development of orientation selectivity is delayed, whereas adaptation orthogonal to a cell's preferred orientation (large $\Delta\theta$) accelerates the development of orientation selectivity. More importantly, however, adaptation near the preferred orientation reduces responses on the near flank of the tuning curve, shifts the preferred orientation away from the adapting stimulus and increases the width of the tuning curve, whereas adaptation far away from the optimal orientation maintains orientation preference and sharpens orientation tuning.

What kind of mechanism could explain the effects of brief adaptation? We propose that adaptation near the cell's preferred orientation could reduce cortical responses due to an orientation-specific depression of feedforward synapses that is maximal near the adapting orientation (Fig 4a). This decrease in responsiveness 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. Could we use the same mechanism, *ie*, orientation-specific depression of feedforward synapses, to explain the effects of orthogonal adaptation? The answer is yes and is supported by the cartoon shown in Fig 4. When the adapting stimulus is presented, synapses "S1" between the neurons tuned to the adapting orientation and those preferring the orthogonal orientation (vertical cell in Fig 4b) would exhibit depression, synapses "S2" originating from the neurons tuned away with respect to the adapting orientation would show less depression, and synapses "S3" originating from the neurons tuned to the orthogonal orientation, inactive during the presentation of

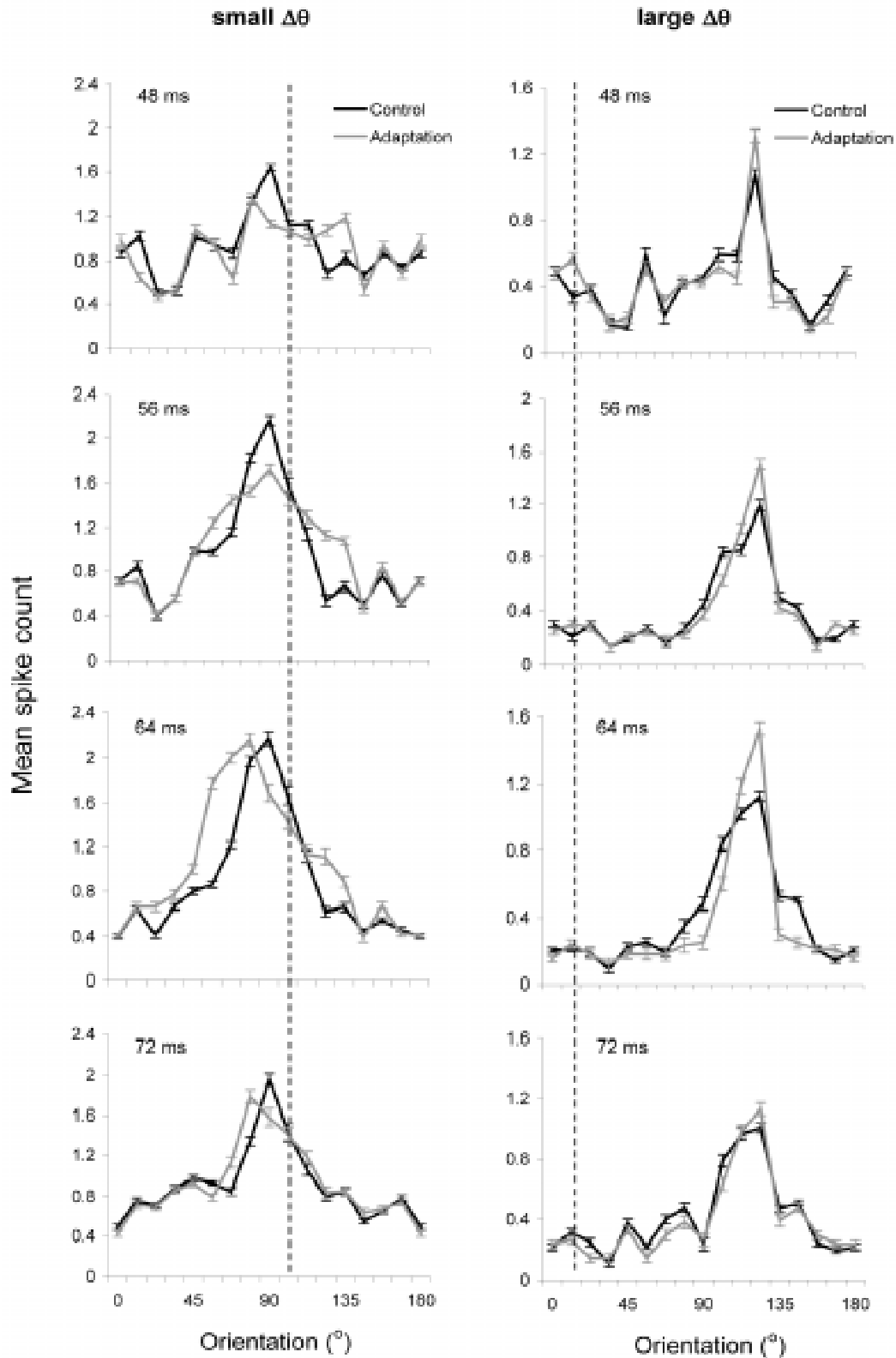


Fig 3 Temporal dynamics of brief adaptation in V1 neurons revealed by reverse correlation. Left: Adaptation near the cell's preferred orientation (small delays the development of orientation tuning, shifts the preferred orientation away from the adapting stimulus, and broadens orientation selectivity. Right: Adaptation at an orthogonal orientation relative to the cell's optimal orientation (large $\Delta\theta$) accelerates the development of orientation tuning, preserves orientation preference, and sharpens orientation selectivity. The graphs within each column show the development of orientation tuning for two neurons at different temporal delays during control (black) and adaptation (grey) conditions. The adapting orientation is marked by the dashed line. Error bars represent SEM

the adapting stimulus, would remain unchanged. This orientation-dependent weakening in the strength of feedforward synapses may affect orientation selectivity. Indeed, when the neuron tuned to the vertical orientation is stimulated at its preferred orientation, its response would remain unchanged because the corresponding feedforward synapses (S3) are not affected by adaptation. However, when the input stimulus is tilted, the response of the vertical neuron decreases because synapses (S2) that carry most of the input stimulus would show some depression. This may lead to a narrowing in the tuning curve of the vertical neuron and, therefore, an increase in orientation discrimination after orthogonal adaptation.

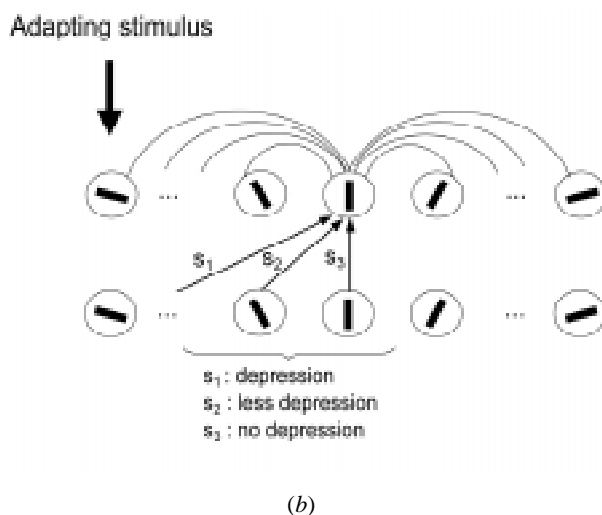
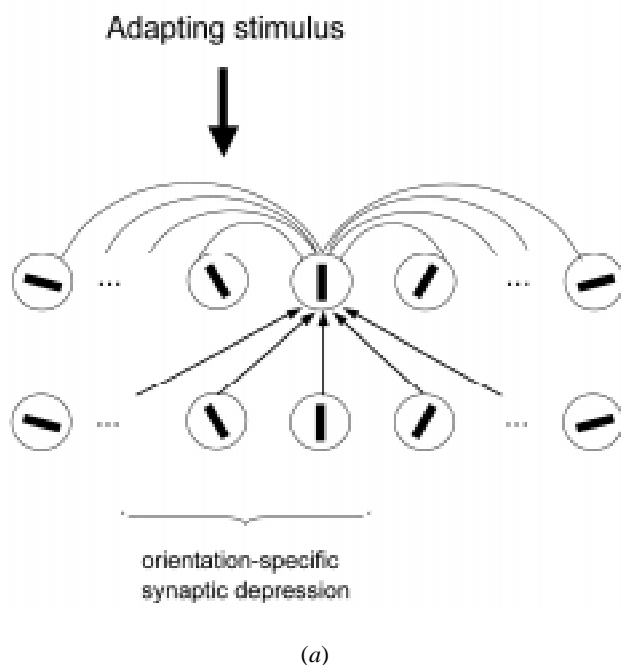


Fig 4 Two-layer neuronal network that could explain the mechanism of orientation adaptation. See text for details

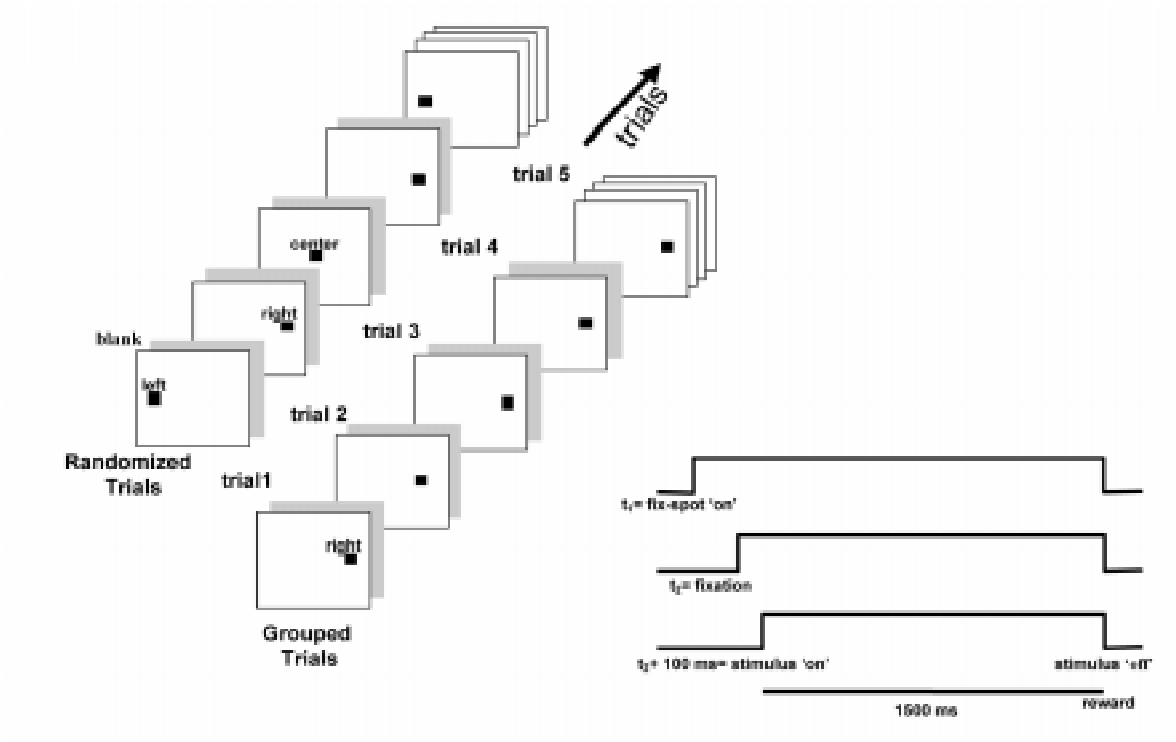
Significance of adaptation-induced orientation plasticity for vision

Explanations of the consequences of rapid adaptation for natural vision are more qualitative at present, but the experimental details now available should allow a full understanding of rapid as well as short-term adaptation. On the one hand, rapid adaptation during the time course of fixation induces a suppression of responses on the flank of the tuning curve toward the adapting stimulus and a facilitation of responses on the opposite flank, which together constitute a repulsive shift in the preferred orientation of V1 neurons. We suggest that brief adaptation improves the discrimination of orientations close to the neuron's optimal orientation by increasing the slope of the tuning curve in the vicinity of the pre-adaptation preferred orientation. This improvement in discrimination performance after iso-orientation adaptation has clear psychophysical support [28,29] and could be a mechanism that might be used by the visual system in order to resolve fine orientation details during visual fixation.

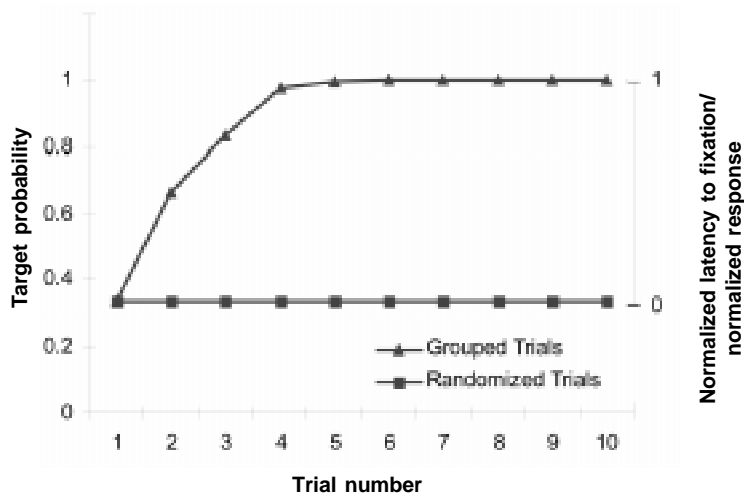
On the other hand, since the mean saccade length during free viewing is relatively large, successive fixations are likely to be made on image patches of dissimilar structure. In this case, adaptation to largely dissimilar image patterns improves neuronal performance in V1 by sharpening orientation tuning curves, and there is a corresponding improvement of psychophysical performance on orientation discrimination. Given the ubiquity of successive saccades to patches of dissimilar structure during natural vision, we suggest that the visual system has adapted to the correlational structure of images so as to encode local features more efficiently.

TOP-DOWN PLASTICITY: INFLUENCE OF AN INTERNAL REPRESENTATION ON ORIENTATION-SELECTIVE V1 RESPONSES

An internal representation of stimulus location is necessary for moving the eyes or for making other visually guided movements. The history of visual stimulation has a key role in acquiring an internal representation: knowledge of where a stimulus would appear next is often based on the temporal statistics of previously viewed stimuli, and is acquired progressively as stimulation proceeds. Most investigations of the control of visually guided movements have focussed on how parietal and frontal cortex, in conjunction with brain stem circuits, are involved in target selection and eye movement control [30-32]. However, recent work from a few laboratories, including ours, have claimed a role for early visual cortex in saccade planning and decision making [33-34]. In a study aimed at examining whether and how neurons are influenced by acquisition of an internal model of stimulus location, we have found an unexpected involvement of V1 - in a manner that is consistent with early visual cortex being part of a distributed network of cortical areas that is involved in



(a)



(b)

Fig 5 Experimental task for examining an internal representation of stimulus location, and the Bayesian probabilities associated with the task (a) Grouped and randomized trials. Trial sequence on left shows an example of randomized trials. In successive trials, the fixation spot (always red) appeared randomly in one of three locations (left, right or center). Sequence to the right shows an example of grouped trials, in which the spot appeared at the same location for a succession of trials. Timing sequences are shown at right. When the fixation spot appeared on a previously blank screen (time t_1), the monkeys made a saccade to the spot (time t_2) and held fixation for 100ms (time t_2+100 ms), following which a stimulus consisting of drifting sinusoidal gratings appeared within a window centered on the fixation spot. The monkeys were required to hold fixation throughout the stimulus presentation (1500 ms) to earn a juice reward. Responses of V1 neurons were recorded during the stimulus presentation time (b) The Bayesian estimate of target probability in the two task conditions. In the grouped sequence, the estimate of the target probability (left ordinate) rises from 1/3 in trial 1 to a value close to 1 by trial 4, while in the randomized sequence, the estimated probability of the target appearing at any location is (on average) 1/3, regardless of trial number. The Normalized Latency to Fixation (calculated as the ratio of the difference in trial by trial fixation latencies in grouped and randomized conditions to the sum of latencies in the two conditions) and the Normalized Response (similarly calculated from trial by trial neuronal responses in the grouped and randomized conditions) closely resemble those predicted by the Bayesian estimates (right ordinate)

acquiring the internal representation [16].

We devised a gaze direction task in which information about future stimulus locations could be obtained in one task condition but not in another. A fixation spot appeared at one of three locations on a computer screen placed in front of a subject (Fig 5a). In one condition, the location of the fixation spot varied randomly from trial to trial (the “randomized” sequence), while in the other, the spot appeared repeatedly at the same location for a succession of trials (the “grouped” sequence). No overt cue was provided as to which sequence was in effect. In the grouped sequence, the Bayesian probability of target appearance at a particular location can be explicitly calculated, and rapidly approaches certainty as trials progress. On the other hand, in the randomized sequence, the probability of target appearance at any of the three locations is constant (equal to 1/3) from trial to trial (Fig 5b).

We asked human subjects to indicate where the target would appear next as trials progressed in either the randomized or the grouped sequence. The probability of successful prediction tracked the target probabilities in both sequences. Similarly, human subjects tracking the appearance of stimuli on a screen showed a significant reduction in reaction time in grouped trials relative to randomized trials. We trained alert monkeys to fixate stably and measured their latency to achieve fixation in the two task conditions. We reasoned that fixation latency would shorten as monkeys attained knowledge of target location, but not otherwise. It has been shown previously that the saccade latency to a visual target is a sensitive indicator of the likelihood of the target’s appearance [35-37]. Indeed, fixation latency was approximately constant from trial to trial in the randomized condition but shortened significantly as trials progressed in the grouped condition, in a manner predicted by the Bayesian probability of target appearance. These findings are consistent with the acquisition of an internal representation of stimulus location with successive trials in the grouped condition of the task, in both humans and monkeys.

Responses of V1 neurons to their preferred stimuli were also modulated significantly in the grouped condition as trials progressed and information about future stimulus location was acquired. V1 neurons are selective for a particular stimulus orientation, and a subset are also robustly modulated by the position of the eyes in the orbits [38-39] that is, V1 neurons can signal the direction of gaze. We found that V1 responses were further modulated by the manner in which stimuli appeared at a particular stimulus location: stimuli appearing in a grouped sequence at one location caused neurons to respond significantly more (or less) than when stimuli appeared randomly, and the response difference tracked the trial-by-trial Bayesian probability of the grouped sequence. In other words, responses to the same visual stimulus (a grating of optimal orientation for a neuron), presented at the same location

(and hence subtending the same angle of gaze), are altered when stimuli are presented in one sequence of trials (the grouped sequence) than when they are presented randomly. Thus, V1 neurons signal in their responses the probability of target appearance, and thereby code an internal representation of stimulus location.

How might V1 neurons dynamically alter their responses to signal an internal representation? The modulation of V1 responses constitutes an active shaping of the orientation tuning curve, for responses to the preferred orientation are specifically and selectively modified as the representation is acquired. Orientation selective responses are similarly modified after visual discrimination learning or during short-term visual memory [40-42]. The response change in V1 neurons during the grouped condition involves the integration of top-down inputs carrying task-dependent signals with bottom-up ones carrying visual signals. Top-down signals are likely to arise from the parietal and frontal cortex, which are known to play a key role in saccade decisions and commands [32,43-45]. Feedback projections from these areas to modulate the strength of recurrent connections between local V1 neurons [46-47] would effectively modify the amplification of feedforward inputs to V1 neurons, and would be a plausible mechanism by which orientation tuning can be altered as trials progress.

CONCLUSIONS

Neurons in the first stage of cortical processing, V1, change their responses as they are stimulated visually (via bottom-up processes) or as task or behavioral conditions change (via topdown influences). Plasticity is an integral part of information processing in the cortex. The findings on orientation plasticity induced by adaptation on the time scale of visual fixation demonstrate that these changes can be rapid and can continuously influence vision. The modulation of V1 responses by an internal representation of stimulus location indicates that even the earliest cortical areas are part of a distributed cortical network involved in moving the eyes and regulating visuomotor behavior.

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