

PLASTICITY OF ORIENTATION PROCESSING IN ADULT VISUAL CORTEX

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Neurons in the primary visual cortex (V1) have been traditionally considered to be passive filters, extracting elementary features of visual stimuli such as local orientation or direction of motion and responding invariantly to the physical properties of stimuli present in their receptive fields. However, another view has emerged in the past 15 years. According to this view, V1 responses are strongly influenced by the spatial and temporal context in which local features are presented, and their responses are modulated as well by previous visual experience, including perceptual learning and adaptation.

Evidence that even the earliest areas of the adult cerebral cortex have the remarkable capacity to change by experience, a phenomenon termed “plasticity”, has been accumulating steadily. The first reports of plasticity in primary sensory cortex of the adult brain came from studies in the somatosensory cortex, which contains a systematic sensory representation of the body surface. Partially removing inputs to the cortex by peripheral nerve transection or by amputation of a finger reorganized the cortical sensory representation such that the denervated cortex now responded to adjacent fingers or the hand (Merzenich et al., 1983, 1984). In V1, sensory map plasticity was first demonstrated using retinal lesions, in which the cortical regions processing inputs from the lesioned parts of the retina were initially silenced, but then regained activity by shifting receptive fields toward regions of the retina surrounding the lesion (Kaas et al., 1990; Gilbert and Wiesel, 1992). Such lesion-induced plasticity implies either the unmasking of existing connections or the formation of new ones (Darian-Smith and Gilbert, 1995). New connections are typically associated with plasticity during development, when neurons are being wired together, but are unlikely to be a mechanism working on shorter time scales in adulthood during normal sensory processing. The latter kinds of plasticity include dynamic changes in neuronal responses and short-term plasticity associated with contextual effects, learning or adaptation.

Dynamics and plasticity of responses in V1

Dynamic effects induced by the spatial context of visual stimuli allow V1 neurons to integrate information from different parts of the visual scene. These effects are manifested when both the classical receptive field, i.e. the receptive field center, and the extraclassical receptive field, i.e. the surround, are stimulated together. The way in which surround stimulation modulates responses elicited by a center stimulus is highly nonlinear and often non-intuitive. Thus, stimuli in the surround can either facilitate or suppress cortical responses depending on the relative orientation and contrast between the center and surround. The presence of a surround stimulus of similar orientation as the cell's preferred orientation suppresses the response to a high-contrast optimal stimulus within the receptive field center and facilitates the response to a low-contrast optimal stimulus within the receptive field center (Toth et al., 1996; Somers et al., 1998; Polat et al., 1998). On the other hand, stimulating the surround with a stimulus whose orientation differs significantly from the cell's preferred orientation facilitates responses to optimal stimulation within the center (Sillito et al., 1995; Levitt and Lund, 1997). In this case, the cell responds 'supraoptimally', i.e., beyond the level expected after stimulation with the optimal orientation.

In addition to integrating inputs from outside their classical receptive fields, V1 responses are also sensitive to the history of visual stimulation, or short-term experience. For instance, masking a portion of the visual field for several minutes (a situation akin to an “artificial scotoma”) while

placing a patterned stimulus around the mask demonstrates the capacity of V1 neurons with receptive fields inside the artificial scotoma to alter their responses. Specifically, after a few minutes of conditioning with the artificial scotoma, the receptive fields of neurons close to the scotoma borders expand beyond their original limits and show an overall increase in responsiveness (Pettet and Gilbert, 1992; Das and Gilbert, 1995; DeAngelis et al., 1995). This type of receptive field plasticity has also been demonstrated at shorter time scales. DeWeerd et al. (1995) have shown that after exposure to a static stimulus consisting of a similar “artificial scotoma” pattern, neurons with receptive fields inside the scotoma borders begin to respond despite the absence of retinal stimulation, a phenomenon associated with the perceptual filling-in effect (Ramachandran and Gregory, 1991).

The dependence of V1 neuron responses on short-term or recent experience is evident in the phenomenon of pattern adaptation: selective exposure for a period of time to patterned stimulation induces transient changes in the selectivity of V1 responses. Pattern adaptation has been characterized with respect to many stimulus dimensions, such as orientation (Blakemore and Campbell, 1969; Hammond et al., 1989; Nelson, 1991; Carandini et al., 1998; Muller et al., 1999; Dragoi et al., 2000), contrast (Movshon and Lennie, 1979; Ohzawa et al., 1982; Carandini and Ferster, 1997; Carandini et al., 1997), spatial frequency (Movshon and Lennie, 1979; Saul and Cynader, 1989), direction of motion (Maffei et al., 1973; Hammond et al., 1985; 1986), and velocity (Hammond et al., 1985).

Cortical neurons also have the adaptive capacity to change their responses with perceptual learning (Gilbert et al., 2001). Perceptual learning in vision is a particular form of plasticity that begins from postnatal life and continues throughout adulthood, and allows us to improve visual performance after active exposure to a structured visual environment. There are many examples in which training has been shown to improve discrimination along a variety of visual stimulus dimensions. For instance, training can improve spatial resolution of the visual system (Poggio et al., 1992; Fahle and Edelman, 1993), the ability to discriminate orientations (Vogels and Orban, 1985; Schoups et al., 2001), the direction of motion (Ball and Sekuler, 1982; 1987), or the depth of visual targets (Fendick and Westheimer, 1983). However, importantly, unlike other forms of learning in which enhanced performance in one task improves performance in related tasks, perceptual learning is highly specific for the stimulus dimension used in the training task, such as retinal position (e.g., Karni and Sagi, 1991) or orientation (e.g., Ramachandran and Braddick, 1973; McKee and Westheimer, 1978). This high degree of specificity has important implications for the neuronal mechanisms underlying perceptual learning, for it argues that plasticity must be a phenomenon present in the early visual cortical areas. Indeed, recent work has demonstrated task-specific learning-induced plasticity of V1 neurons, in animals trained to perform either a three-line bisection task (Crist et al., 2001) or an orientation discrimination task (Schoups et al., 2001).

Orientation plasticity in V1

A prominent form of plasticity in the adult visual cortex is the plasticity of orientation tuning. Orientation plasticity 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 (Gibson, 1933; Gibson and Radner, 1937; Magnussen and Kurtenbach, 1980). At longer time scales, the ability of the visual

system to discriminate differences in orientation can be improved through perceptual learning. This suggests that visual experience or learning could alter the functional properties of orientation-selective neurons and networks in the early visual cortex of the adult brain.

V1 neurons are selective for the orientation of lines which are presented in their receptive field center (Hubel and Wiesel, 1962). The development of orientation tuning does not require visual experience (Hubel and Wiesel, 1963; Fregnac and Imbert, 1978; Godecke et al., 1997; Crair et al., 1998), although selective experience in early life can modify the orientation preference of neurons (Blakemore and Cooper, 1970; Hirsch and Spinelli, 1970; Blakemore, 1977; Stryker et al., 1978; Sengpiel et al., 1999). The orientation preference of adult V1 neurons has long been considered a stable property that remains fundamentally unchanged after early life. However, recent evidence demonstrates that orientation selectivity of neurons and the way in which orientation is mapped onto the cortex can be altered by visual experience, and these changes have important consequences for visual perception.

There are several ways by which orientation plasticity has been demonstrated in adult V1 neurons. While the details of the inducing procedures define the specifics of cortical plasticity, three major types of orientation plasticity stand out (Figure 1):

(i) *Adaptation-induced plasticity*. Continuous visual stimulation for a period of seconds to minutes (a process defined as adaptation) at a fixed orientation induces a reversible shift in the preferred orientation of individual neurons, away from the adapting stimulus (Figure 1A; Muller et al., 1999; Dragoi et al., 2000). Interestingly, this form of short-term plasticity induces not only a significant change in optimal orientation but also a reorganization of responses around the new preferred orientation. For instance, a long period of adaptation induces a reduction of responses on the flank of the tuning curve near the adapting stimulus and a facilitation of responses on the opposite flank. This suggests that adaptation-induced orientation plasticity involves an active process of network synaptic changes that lead to a new preferred orientation rather than simply a passive reduction of orientation selective responses around the adapting orientation.

(ii) *Stimulation timing-dependent plasticity*. Intracortical electrical stimulation paired with visual stimulation for several hours leads to a shift in the preferred orientation of individual neurons (Figure 1B; Schuett et al., 2001). The shift can occur toward or away from the orientation of the visual stimulus depending on the timing between the visual stimulus and the delivery of the electrical pulses. Consistent with previously demonstrated rules of synaptic plasticity based on the precise timing of the presynaptic and postsynaptic activity (spike-timing-dependent plasticity) obtained in slice preparations (Markram et al., 1997; Zhang et al., 1998), electrical stimuli delivered after the visual stimulus driven activity reaches cortex produces a shift in the preferred orientation of individual neurons toward the visually presented orientation, whereas reversing the temporal order between electrical and visual stimuli produces a shift in preferred orientation away from the visual orientation. Except for the timing between stimuli, this pairing protocol is similar to that introduced by Fregnac et al. (1988) in which the preferred orientation of individual neurons shifted toward the the orientation of the visual stimulus. Similarly, the preferred orientation of individual neurons can be induced to shift toward the orientation at a cortical site that is stimulated pharmacologically (Toth et al., 1997) or electrically (Godde et al., 2002), even without a paired visual stimulus. However, the rules of synaptic plasticity underlying such shifts are likely to still involve the relative timing and correlations between input and output

spikes of neurons. Yao and Dan (2001) specifically demonstrated that two gratings – one at a tilted orientation and the other at the cell's preferred orientation – flashed in quick succession (8 - 40 msec apart) causes a cell to shift its preferred orientation towards the first grating, whereas flashing the gratings in the opposite order causes the cell to shift its orientation away from the first grating.

(iii) *Learning-induced plasticity*. Intensive practice in discriminating fine orientation differences increases neuronal orientation discrimination performance at the trained orientation (Vogel and Orban, 1985; Shiu and Pashler, 1992), but not at other orientations or visual field locations (Schoups et al., 1995). The proposed mechanism for this type of plasticity has been linked to the observed increase in the slope of the tuning curve of individual V1 neurons in the vicinity of the trained orientation (Figure 1C; Schoups et al., 2001).

All these forms of orientation plasticity demonstrate the powerful effect of short- and long-term synaptic plasticity rules, such as those previously derived from work in reduced preparations including cultured neurons and brain slices, on shaping fundamental properties of individual V1 neurons and networks *in vivo*. Two directions have recently emerged from our understanding of cortical plasticity: how is orientation plasticity represented across the cortex, and what is its significance for visual perception, including natural vision? Whereas orientation plasticity induced by electrical stimulation does not appear to have a direct impact on vision, adaptation and learning-induced changes in V1 responses offer powerful tools with which to address both questions. In the following sections, we will focus on plasticity of orientation tuning induced by adaptation as a model system in which to understand the representation, mechanism and significance of plasticity in V1 networks.

Adaptation-induced orientation plasticity

Our knowledge of adaptation in early visual cortex comes from studies demonstrating that exposure to a potent stimulus for several minutes (pattern adaptation) can cause a reduction in sensitivity to stimulus attributes such as contrast or spatial frequency (Blakemore and Campbell, 1969; Movshon and Lennie, 1979; Ohzawa and Freeman, 1982; Nelson, 1991; Carandini et al., 1998). 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 (Carandini and Ferster, 1997) due to synaptic depression (Abbott et al., 1997; Chance et al., 1998) or to a slow hyperpolarizing membrane potassium current (Sanchez-Vivez et al., 1998).

In a recent study, Dragoi et al. (2000) 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 reorganization of the entire profile of the orientation tuning curve. Figure 2A shows how the preferred orientation of a 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 preferred orientation, and a final period of recovery. When the difference between the cell's preferred orientation and that of the adapting stimulus (??) is -22.5° , i.e. the adapting orientation is on the left flank of the tuning curve, 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 ($\theta = 45^\circ$), 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 2B 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 (Dragoi et al., 2000). 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 (Figure 2C).

Orientation plasticity and the cortical map of orientation

Adaptation-induced orientation plasticity is a cortical phenomenon that depends on changes in inputs from other neurons in a local network. Thus, it is conceivable that the strength of adaptation effects would depend on the specific cortical location of a neuron within the map of orientation preference. V1 neurons are clustered according to their orientation preference in iso-orientation domains (Hubel and Wiesel, 1974), where the optimal orientation of individual neurons varies smoothly across the cortex, and singularities or pinwheel centers (Bonhoeffer and Grinvald, 1991; Blasdel, 1992), which are foci where the optimal orientation of neurons varies rapidly (Figure 3A). The structure of the orientation map in V1 implies that the orientation distribution of local connections would vary with a neuron's position within the map: neurons in pinwheel centers are likely to be connected to neurons of a broader range of orientations than neurons in iso-orientation domains. This suggests that altering the efficacy of intracortical orientation-specific inputs to neurons in different locations of the orientation map in a manner that induces adaptive changes in tuning properties could show dependence on cortical location.

Dragoi et al (2001) investigated the relationship between adaptation-induced orientation plasticity and a neuron's location in the orientation preference map in V1 of adult cats. Optical imaging of intrinsic signals was used to obtain the orientation map in a patch of V1, and then the vascular pattern of the cortical surface was used in relation to the orientation map to guide electrode penetrations aimed at iso-orientation domains or pinwheel centers (Figure 3A). The specific question was whether the local orientation distribution at the recording site correlated with the degree of plasticity. Anatomical and physiological data in V1 (Hata et al., 1991; Weliky et al., 1995; Kisvarday et al., 1997; Das and Gilbert; 1999) has demonstrated that local excitatory and inhibitory inputs to cortical cells originate from within ca. 500 μm radius around the cell body. The critical feature for explaining orientation plasticity was found to be the distribution of local inputs to individual neurons. When the recording site is in the middle of an iso-orientation domain (Figure 2B), neurons within a 500 μm radius have a preponderance of orientation preferences similar to the recorded neuron, whereas when the recording site is near a pinwheel center local inputs arise from domains of all orientations. Qualitatively, the orientation distribution of inputs to a neuron is a predictor of the degree of change in its orientation preference. When it has a peaked profile, adaptation induces only minor changes in orientation

selectivity (Figure 3B), whereas the orientation tuning curve undergoes pronounced changes when the orientation distribution is flat.

What kind of mechanism could generate these effects? The changes in orientation selectivity following adaptation imply a network mechanism that reorganizes responses across a broad range of orientations. For instance, hyperpolarization of neurons at or close to the adapting orientation, due to either membrane mechanisms (such as slow hyperpolarizing Ca^{++} and Na^{+} activated potassium channels; Sanchez- Vives et al., 2000) or to synaptic depression (Abbott et al., 1997) can cause suppression of responses on the near flank of the tuning curve, whereas facilitation of responses on the far flank requires disinhibition (Dragoi and Sur, 2000) and possibly amplification via local excitatory intracortical interactions (Somers et al., 2002). But what is important is that the strength of these effects, which determines the magnitude of the change in preferred orientation, depends on the location of neurons in the orientation map. Neurons in an iso-orientation domain would be only weakly activated by intracortical inputs with orientations that differ from the domain's preferred orientation, whereas neurons located at or near pinwheel centers would receive strong local inputs from neurons of all orientations. Therefore, altering the efficacy of these inputs through adaptation is likely to induce more profound changes in the orientation preference of neurons at or near pinwheel centers. This suggests that adaptation-induced orientation plasticity in V1 is an emergent property of a local cortical network overlaid on a non-uniform orientation map.

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 (see below), but the tilt aftereffect leads to an altered perception of contour orientation.

Two recent studies have demonstrated that the discrimination of orientations is actually improved by adaptation. Clifford et al (2001) showed that orientation discrimination around vertical improved in human observers after adaptation to either vertical or horizontal gratings but was impaired after adaptation to intermediate orientations. The improvement was greatest when the adapting and test gratings were orthogonal. The study, however, employed long adaptation times of several seconds to a minute, a duration unlikely to have an adaptive role in ongoing, natural vision.

Dragoi et al (2002) asked whether cortical plasticity is involved during the rapid processing of image patterns during natural viewing. During the viewing of a natural scene, we make saccadic eye movements several times a second (Yarbus, 1967; Andrews and Coppola, 1999). 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 (Attneave, 1954; Barlow, 1990). 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 (Figure 4). 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?

Dragoi et al. showed 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. They also showed that rapid adaptation 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 (Nelson et al., 1991; Muller et al., 1999) 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 reverse correlation procedure (de Boer and Kuyper, 1968; Ringach et al., 1997; Dragoi et al., 1999; Mazer et al., 2002). Dragoi et al thus measured how the orientation tuning of V1 neurons evolves at the millisecond time scale before and after brief adaptation. They 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 5 shows two examples of cells with distinct behaviors during brief adaptation. When the adapting stimulus orientation is near a cell's preferred orientation (small ??), the development of orientation selectivity is delayed, whereas adaptation orthogonal to a cell's preferred orientation (large ??) 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.

Significance of adaption-induced orientation plasticity for vision

These effects of rapid adaptation (with the adapting grating presented for hundreds of msec) on neuronal responses are fundamentally similar to the effects of short-term adaptation (with the adapting grating presented for seconds to minutes). In both cases (compare Figure 1A or the bottom part of 3B, and Figure 5), adaptation with a grating oriented near a cell's preferred orientation alters the tuning curve and broadens selectivity, whereas a grating oriented orthogonal to a cell's preferred orientation preserves the same orientation preference but sharpens selectivity (Dragoi et al., 2000; 2002). How do these neuronal changes explain the perceptual consequences of short-term or rapid adaptation?

Population coding models that relate neuronal responses to perception assume that a cell is a "labeled line" for a stimulus, so that each neuron signals the presence of its preferred stimulus within its receptive field. The response of the population is inferred as the sum of the individual neuron responses (Sur et al., 2002). Two of the response changes induced by short-term adaptation - reduction in response at the adapting orientation and broadening of tuning width - are important for explaining the repulsive tilt aftereffect (at intermediate orientation differences between adapting and test orientations) and a smaller attractive aftereffect at large orientation differences (Clifford et al., 2001).

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 (Regan and Beverley, 1985; Clifford et al., 2001) 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.

Conclusions

Examining how visual cortical neurons adapt their response properties to short-term exposure to patterned stimulation or to perceptual learning, and how the capacity for adaptive changes is mapped onto the cortex, is fundamental for understanding neuronal mechanisms of conscious visual perception. An astonishing property of adaptation-induced plasticity is the fact that its magnitude changes depending on cortical location. This suggests that the visual cortex is not homogeneous in its capacity to undergo plastic changes and indicates the existence of a map of orientation plasticity, closely related to the map of orientation preference, in which pinwheel centers constitute foci of maximal plasticity and the rate of orientation change is a measure of the degree of plasticity across V1. It remains an open and interesting question as to whether there are similar plasticity maps related to other functional maps, such as those for eye preference, spatial frequency, direction, or the effects of attention.

Plasticity is an integral part of information processing in the cortex. Visual cortex neurons change their responses as they are stimulated, and vision is continually shaped by these response changes. The findings on orientation plasticity induced by adaptation on the time scale of visual fixation demonstrate that these changes can be rapid indeed and can continuously influence vision.

Figure Captions

Figure 1. Different forms of orientation plasticity in V1. (A) Adaptation-induced orientation plasticity. Short-term exposure for a period of seconds to minutes induces a repulsive shift in the preferred orientation of V1 neurons away from the adapting stimulus (arrow). The solid line represents the orientation tuning curve before adaptation and the dotted line represents the tuning curve after adaptation. (B) **Stimulation timing-dependent** orientation plasticity. The figure schematically shows orientation plasticity induced by a combination of cortical microstimulation and visual stimulation. When electrical microstimulation is delivered to a cortical site 65 ms after the visual stimulus (arrow) there is a shift in the preferred orientation of V1 neurons toward the visual stimulus orientation (a), whereas when electrical microstimulation is delivered after the visual stimulus there is a shift in preferred orientation away from the visual orientation (b). The solid line represents the tuning curve before microstimulation and the dotted lines represent the tuning curves after forward (a) and backward (b) microstimulation. (C) Learning-induced orientation plasticity. Improvement in orientation discrimination performance during learning is accompanied by an increase in the slope of the tuning curve near the trained orientation (arrow). The solid line represents the orientation tuning curve of a V1 neuron before training. The straight solid line represents the slope of the tuning curve at the trained orientation before training; the straight dashed line represents the slope of the tuning curve at the trained orientation after training.

Figure 2. 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.

Figure 3. Adaptation-induced plasticity of orientation tuning and the orientation architecture of V1. (A) Composite orientation map obtained by intrinsic signal optical imaging. The angle of preferred orientation of each pixel is shown in pseudo-color according to the key at top. The circles show the location of 7 representative neurons to illustrate the range of orientation distributions in recorded neurons. (B) Relationship between the local orientation distribution at the recording site and the degree of orientation plasticity. Left: Two recording sites (filled circles) placed respectively within an iso-orientation domain and in a pinwheel center. The white dotted circle of radius 500 μ m represents the basin of local intracortical inputs. Middle:

The percentage of pixels at each orientation within 500 μm of the recording site, after pooling the pixels into eight orientation bins between 0 and 180 deg. The grey curve represents the best 3rd order polynomial fit to each histogram. Right: Orientation tuning curves in the control condition (black) and after adaptation (grey) for the cells recorded at the locations shown in the left panels. The adapting orientation is marked by the grey arrow. Error bars represent S.E.M.

Figure 4. 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.

Figure 5. 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 $??$) 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 S.E.M.

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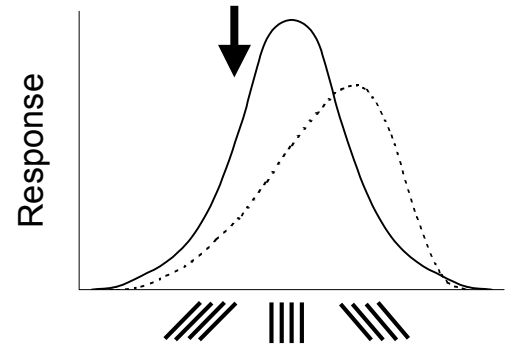
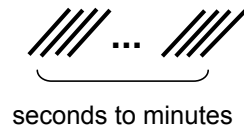
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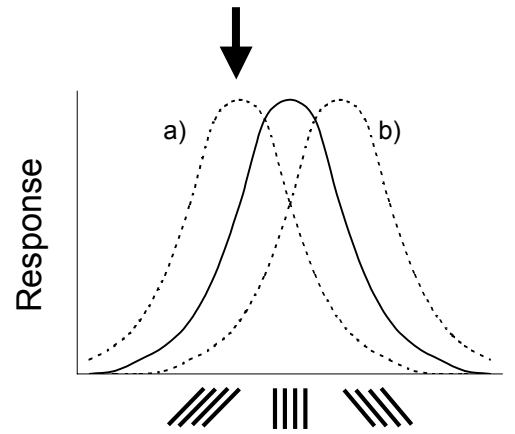
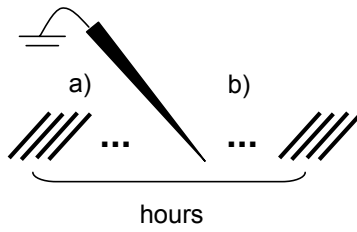
A

*ADAPTATION-INDUCED
PLASTICITY*



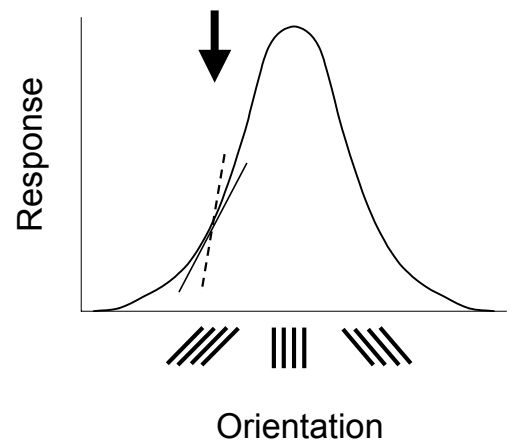
B

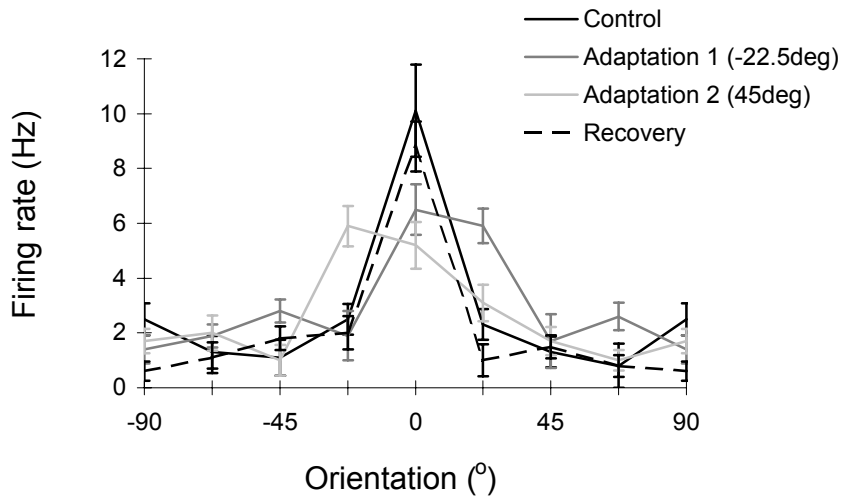
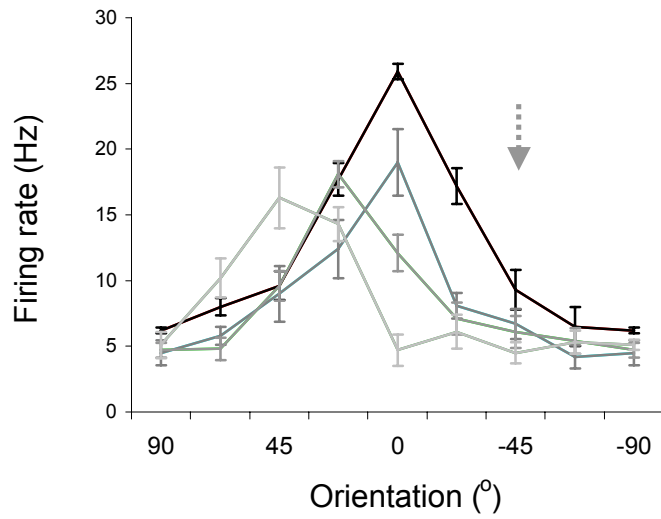
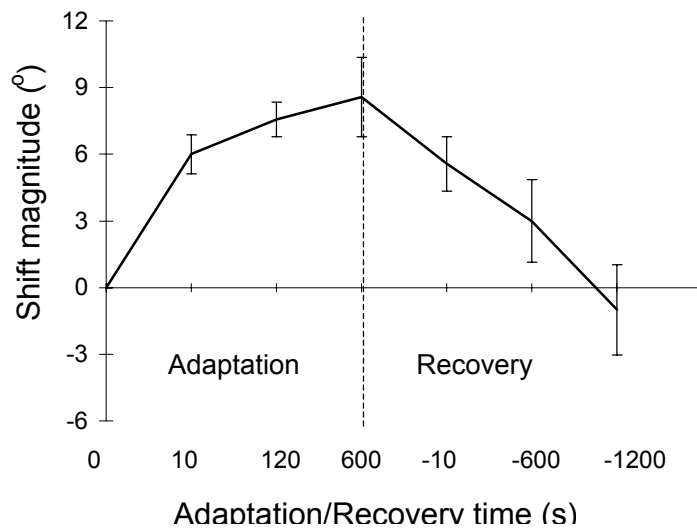
*STIMULATION TIMING-
DEPENDENT PLASTICITY*

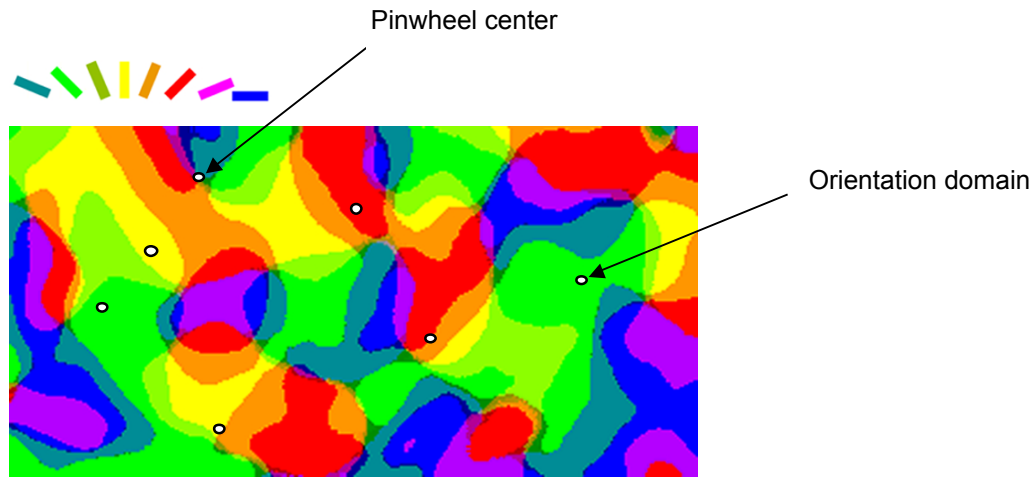
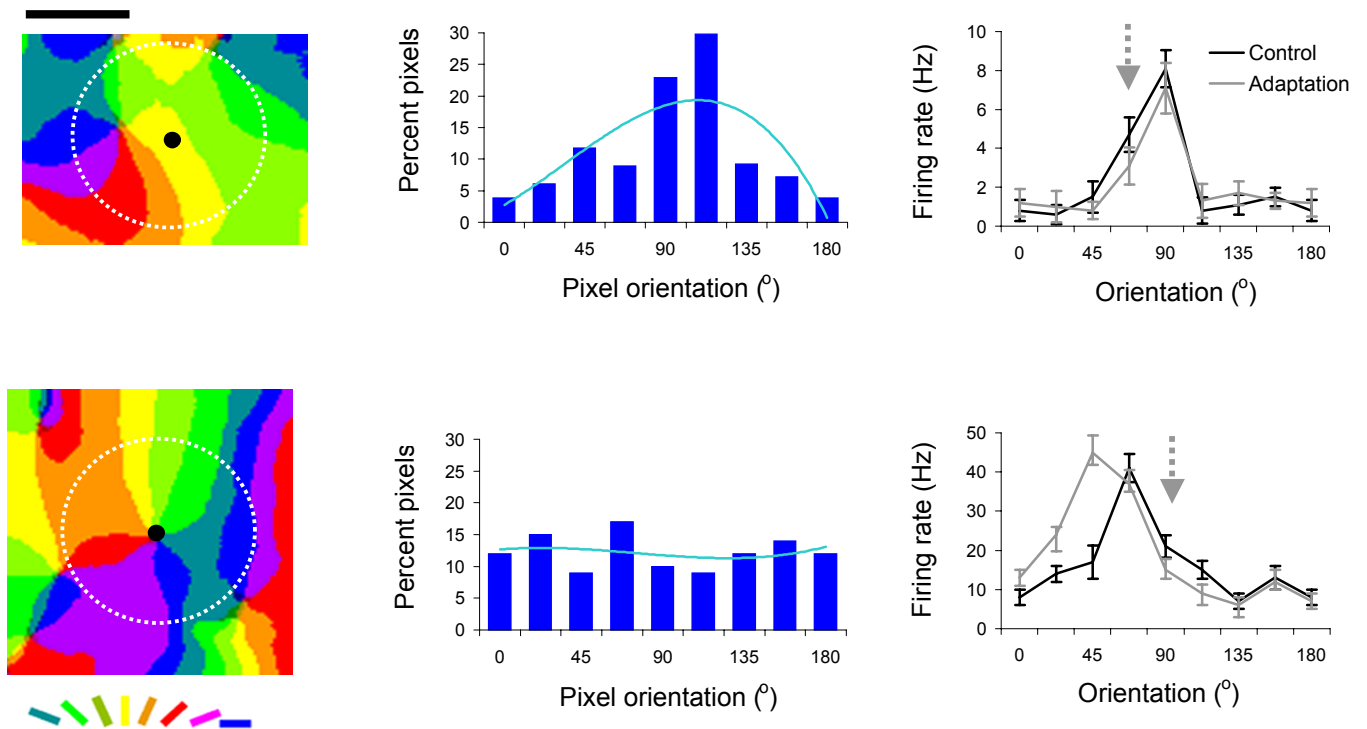


C

*LEARNING-INDUCED
PLASTICITY*



A**B****C**

A**B**



1°

small $\Delta\theta$

large $\Delta\theta$

