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Adaptation changes the direction tuning of macaque MT neurons

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Prolonged exposure to a stimulus, called 'adaptation', reduces cortical responsiveness. Adaptation has been studied extensively in primary visual cortex (V1), where responsivity is usually reduced most when the adapting and test stimuli are well matched. Theories about the functional benefits of adaptation have relied on this specificity, but the resultant changes in neuronal tuning are of the wrong type to account for well-documented perceptual aftereffects. Here we have used moving sinusoidal gratings to study the effect of adaptation on the direction tuning of neurons in area MT in macaques. Responsivity in MT is maintained best in the adapted direction and is strongly reduced for nearby directions. Consequently, adaptation in the preferred direction reduces the direction-tuning bandwidth, whereas adaptation at near-preferred directions causes tuning to shift toward the adapted direction. This previously unknown effect of adaptation is consistent with perceptual aftereffects and indicates that different cortical regions may adjust to constant sensory input in distinct ways.

Prolonged inspection of a strong visual stimulus produces vivid visual aftereffects, in which stimuli similar to the adapting stimulus are perceived to be more different from the adapter than they truly are. 'Repulsive' aftereffects of this type are well known for stimulus orientation[1,2], curvature[3], position[4], spatial frequency[5] and direction of motion[2,6–8]. Adaptation reduces neuronal responsivity in V1, where the strongest effects are generally observed for stimuli that are similar to the adapter. A consequence is that adaptation on the flank of a tuning curve causes a repulsive shift in neuronal tuning away from the adapted value. Such shifts have been found in V1 for spatial frequency[9,10], temporal frequency[11] and orientation tuning[12–16]. Although it might seem that these repulsive neuronal aftereffects match the repulsive perceptual effects, the neuronal findings are in fact opposite to those needed to predict the perceptual phenomena[17–19].

Consider the distribution of activity elicited by a particular stimulus across a population of tuned cells. Before adaptation, peak activity is elicited from cells that are tuned to the stimulus. Suppose that adaptation with a nearby stimulus shifts the tuning curves of these cells away from the adapter. The stimulus that activates them most strongly will now be further from the adapter than it was before adaptation. If neurons always carry the unadapted perceptual 'label', then more remote test stimuli will be perceived as though they are closer to the adapter. Thus, repulsive neuronal aftereffects predict not repulsive but attractive perceptual effects, which are almost never observed. Partly because of these discrepancies, current theories about the role of adaptation in sensory information processing have focused on potential improvements in representational efficiency offered by repulsive shifts in neuronal tuning[20–23] rather than on exploring the relationship between physiological and psychophysical effects.

Repulsive shifts in tuning have been found only in V1, and the effect of adaptation on neuronal selectivity in higher cortical areas is unknown. Here we report on the direction specificity of adaptation in area MT, an extrastriate area containing a high proportion of direction-selective cells[24,25] that has a clearly established role in the perception of visual motion[26–28]. We have previously found that adaptation in MT alters neuronal contrast sensitivity but has relatively little effect on response magnitude[29].

In evaluating the direction specificity of adaptation, we found that adaptation affects MT differently from V1: responsivity is maintained best for stimuli moving in the adapted direction and is strongly reduced for nearby directions. As a result, after adaptation near the preferred direction, direction tuning becomes significantly narrower. Adaptation on the flank of the tuning curve causes an attractive shift of tuning toward the adapted direction. This previously unknown effect of adaptation in MT predicts strong repulsive perceptual aftereffects and suggests that current theories about the functional benefits of adaptation, and mechanistic explanations of their basis, are incomplete because they are based on effects observed in V1 that may not be found in other cortical areas.

RESULTS

We studied 71 well-isolated MT units in 12 anesthetized, paralyzed macaque monkeys. All cells had receptive fields centered within 25° of the fovea, and most receptive fields were within 15°. We evaluated the effect of adaptation on direction tuning by comparing the response to full-contrast sine-wave gratings drifting in 16 test directions (in 22.5° steps) before and after 40 s of adaptation (**Fig. 1**). Top-up adaptation stimuli (5 s) were presented between each pair of

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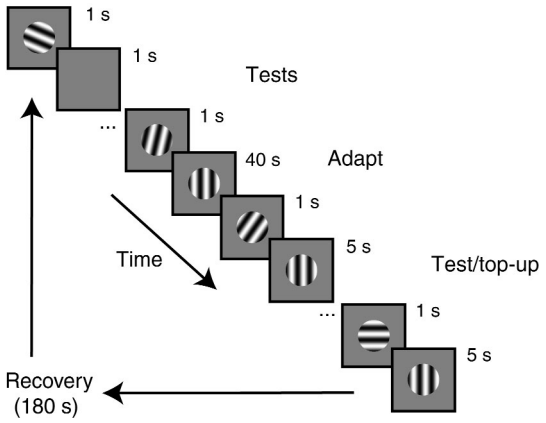

Figure 1 Diagram of the adaptation protocol. Responses to gratings drifting in 16 different directions were measured before and after adaptation to a grating drifting in the preferred, flank or null direction for 40 s; the adaptation level was maintained by 5-s 'top-up' stimuli preceding each test stimulus.

postadaptation test stimuli. The size, spatial frequency and drift rate of the test, adaptation and top-up gratings were identical and were optimized for each cell.

We explored the effect of adapting at a range of directions relative to the preferred direction of MT cells. Below, we present the effect of adapting near the peak preference of the cell, on the flank of the tuning curve, or in directions that failed to evoke a significant response in the cell. We conclude by combining these data sets to show how MT tuning is affected by adaptation over a continuous range of directions.

Preferred adaptation

We defined preferred adaptation to be when the adaptation grating was within 20° of the cell's preferred direction. For the MT cell whose data are shown in **Figure 2a**, adaptation in the preferred direction of the cell caused the peak response to decrease from 89 impulses per second (ips) to 72 ips. The response to nearby directions was reduced more strongly: from 48 to 4 ips at –22° and from 78 to 21 ips at +22°. For the cell in **Figure 2b**, the response to the preferred stimulus increased after adaptation, whereas the response to other directions was reduced.

To quantify the effect of preferred adaptation on direction tuning, we fitted the pre- and postadaptation data of each cell with von Mises functions (Methods). From these fits, we extracted three parameters: the direction evoking the strongest response (preferred direction), the full width of the peak at half height (tuning bandwidth) and the difference between the maximum response and the spontaneous activity (responsivity). The fits for pre- and postadaptation responses for the cell shown in **Figure 2a** indicated that adaptation had little effect on the preferred direction (a shift of 3.7°) or responsivity (reduced from 87 to 70 ips) but reduced the tuning bandwidth from 62° to 32°. For the cell in **Figure 2b**, the preferred direction shifted by 1.1°, responsivity increased from 32 to 39 ips and bandwidth decreased from 122° to 56°.

Our 'preferred' adapting stimuli were not always exact and could be up to 20° from the true preferred direction. Although the preferred direction of most cells was not substantially altered by preferred adaptation, there was a slight tendency for the preferred direction to shift toward the adapted direction: the mean shift was 2.3° ± 1.2° in the attractive direction (indicated by negative values in **Fig. 2c** and hereafter; $P = 0.07$ for difference from a shift of 0).

On average, adaptation reduced the responsivity of MT cells slightly. The geometric mean ratio of post- to preadaptation responsivity was 0.70 (**Fig. 2d**; $P = 0.004$ for difference from 1), with the mean response reduced from 45 to 31 ips. Responsivity in nearby directions, however, was reduced more strongly. For example, for stimuli 12–33° from the preferred direction, the average response decreased from 38 to 13 ips; and for stimuli 34–56° from the preferred direction, it decreased from 24 to 6 ips (data not shown). The consistently stronger reduction in responsivity for nearby directions caused a substantial and consistent narrowing of tuning bandwidth, which

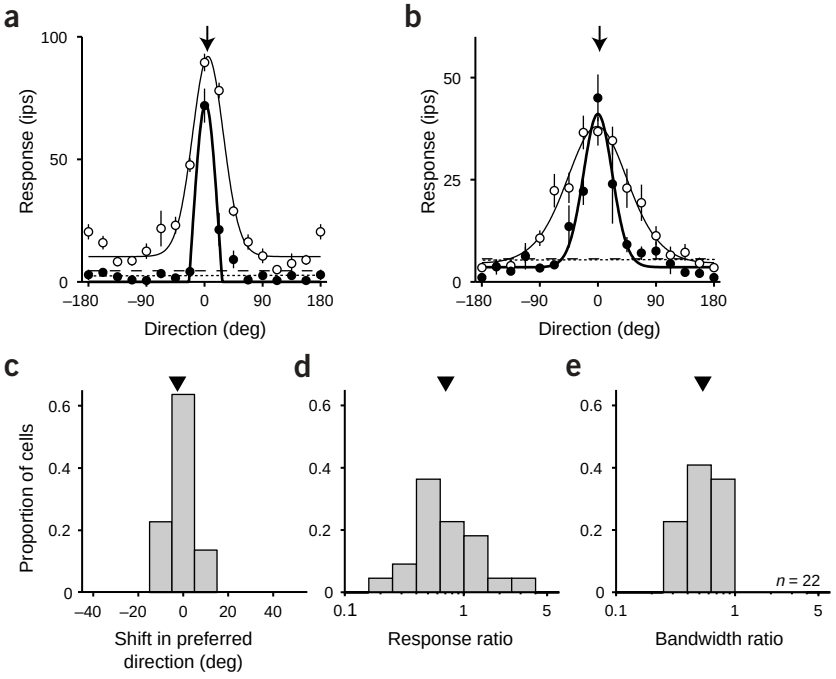

Figure 2 Effect of adaptation in the preferred direction on the direction tuning of MT cells. (**a**) Direction tuning of an example MT cell before (□) and after (■) preferred adaptation (direction indicated by arrow). Dashed and dotted line indicate the spontaneous firing rate before and after adaptation, respectively. Adaptation reduces responsivity slightly and causes a narrowing of tuning bandwidth. Error bars indicate the s.e.m. (**b**) Preferred adaptation in a second MT cell. Responsivity in the adapted direction increases, and tuning bandwidth decreases substantially. (**c**) Histogram of shifts in preferred direction after preferred adaptation for a population of MT cells ($n = 22$). Arrowhead indicates the mean shift, which is not statistically distinguishable from 0. Negative values indicate a shift toward the adapted direction (see text). (**d**) Distribution of responsivity ratios (postadaptation/preadaptation), which on average are below 1. (**e**) Distribution of tuning bandwidth ratios (postadaptation/preadaptation) shows that preferred adaptation reduces tuning bandwidth.

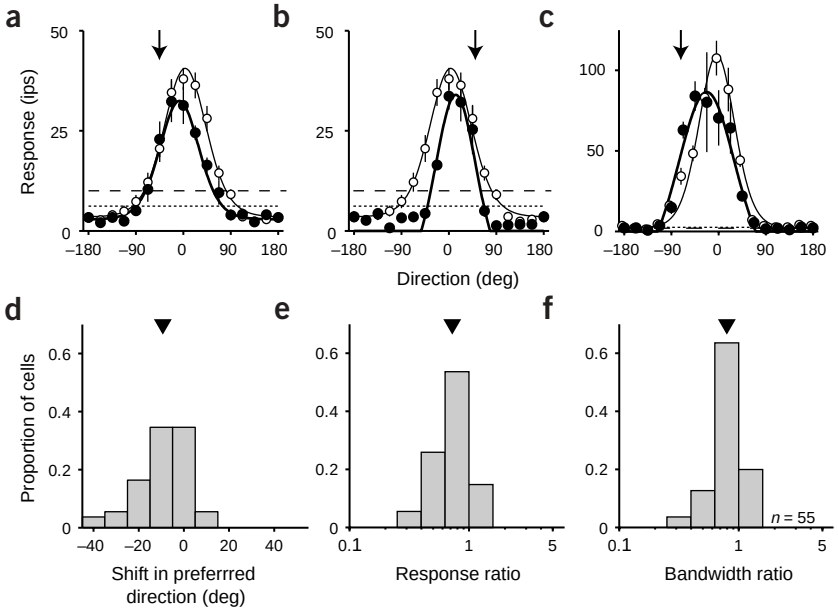

Figure 3 Effect of flank adaptation on the direction tuning of MT cells. (**a**) Direction tuning of an MT cell before (○) and after (●) flank adaptation (direction indicated by arrow). Tuning is shifted toward the adapted direction, and responsivity and bandwidth are reduced. (**b**) Adapting the cell shown in **a** on the opposite flank of the tuning curve results in an opposite shift in preferred direction. (**c**) Adaptation in a second MT cell causes an increase in responsivity on the adapted flank and a strong attractive shift in the preferred direction. (**d**) Distribution of shifts in the preferred direction after flank adaptation for a population of MT cells ($n = 55$). Arrowhead indicates the mean shift, which is significantly different from 0. Negative values indicate a shift toward the adapted direction (see text). (**e**,**f**) Flank adaptation also slightly reduces responsivity (**e**) and tuning bandwidth (**f**).

was on average about half as broad after adaptation as before (**Fig. 2e**; mean bandwidth ratio of 0.54).

Flank adaptation

Our finding that the smallest response decrement occurs for stimuli that are similar to the adapted direction suggested that adaptation in a direction displaced from the preferred direction (on the flank of the tuning curve) would result in a shift of the preferred direction toward the adapted direction. We evaluated the effect of flank adaptation on MT neurons using stimuli 20–75° degrees away from the preferred direction of the cells, choosing an adaptation direction for each cell that evoked a response that was roughly one-half of the peak value (average 42%).

An example of the effect of flank adaptation is shown in **Figure 3a**: adaptation had a negligible effect on the response to stimuli on the adapted flank of the tuning curve, but there was a substantial reduction in responsivity on the opposite flank, causing the preferred direction to shift toward the adapted direction by 10.9°. After a recovery period in which the tuning curve recovered to its original form, we adapted the cell on the opposite flank and observed a shift in the opposite direction of 9.5° (**Fig. 3b**). The effect of flank adaptation for a second, exceptional cell is shown in **Figure 3c**: the response near the adapted direction (–75°) increased strongly in this cell, causing an attractive shift in the preferred direction of 18.3°.

The distribution of shifts in the preferred direction for our population of cells ($n = 55$; **Fig. 3d**) showed an average shift toward the adapted direction of 9.3 ± 1.4° ($P < 0.001$). For 16 cells that were adapted twice, once on each flank (**Figs. 3a**,**b**), the average shifts were attractive for both conditions (12.1 ± 3.4°, $P < 0.001$; 6.7 ± 2.1°, $P = 0.003$). We observed similar shifts when the direction preference was calculated directly from the measured responses by using a vector sum metric[30] rather than the von Mises fits. Attractive shifts in the preferred direction were produced by a well-maintained, or in some cells enhanced (18 of 55 cells), response in the adapted direction and a strongly reduced response for equally potent stimuli from the opposite flank (see below).

The reduction in peak responsivity was intermediate between the effect on the two flanks (**Fig. 3e**; geometric mean ratio of 0.72; $P < 0.001$). Finally, the direction-tuning bandwidth was reduced after flank adaptation, although the effect was substantially weaker than it was for preferred adaptation (**Fig. 3f**; geometric mean ratio of 0.80; $P < 0.001$). We conclude that, as with preferred adaptation, the response is reduced less strongly in the adapted direction than in other nearby directions, thereby causing attractive shifts in direction tuning.

We evaluated the effect of adaptation by using a continuous stimulus sequence without temporal gaps between stimuli. We considered that our finding that responsivity was reduced least for well-matched test and adapt stimuli might be due in some way to stimulus transients at the transition from adapting stimuli to test stimuli of different directions. To confirm that these transients were not affecting our results, we verified in several control cells that similar effects occurred when we added a stimulus blank of 250 ms before each test stimulus. We also found that removing the initial 300 ms of neuronal response to each stimulus made no systematic difference to our results. Finally, in many cells the adapted direction lay between two test directions so that each test stimulus involved a similar transient (**Fig. 3c**).

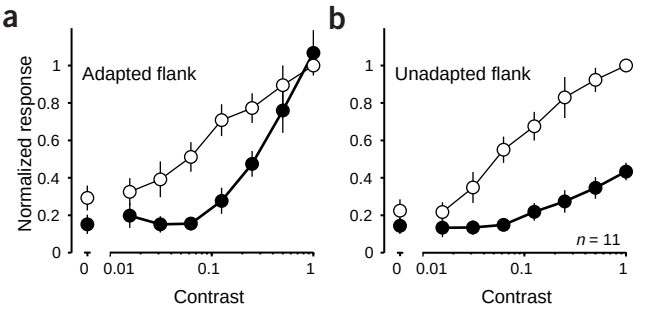

Figure 4 Effects of flank adaptation on responses to targets of different contrast. (**a**) Population contrast response function before (○) and after (●) flank adaptation. Contrast sensitivity is reduced, but the response at full contrast is maintained. (**b**) Population contrast response function for stimuli on the unadapted flank shows that responsivity is strongly reduced at all test contrasts, owing to a change in both contrast and response gain.

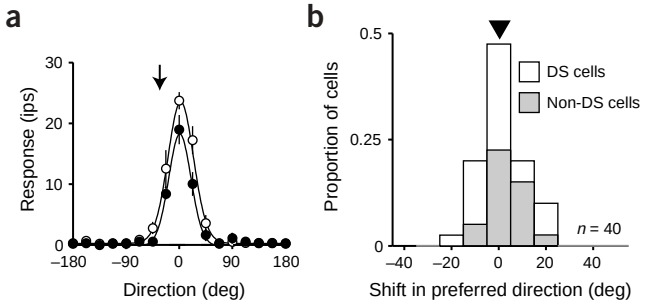

Figure 5 Flank adaptation of V1 complex cells does not cause shifts in tuning. (**a**) A V1 cell whose preferred direction is not altered by flank adaptation (direction indicated by arrow). ○, before adaptation; ●, after adaptation. (**b**) Population histograms for shifts in the preferred direction of direction-selective (DS; $n = 22$) and orientation of non-direction-selective (non-DS; $n = 18$) complex V1 cells after flank adaptation. There is, on average, no shift in the tuning of V1 cells.

Effect of flank adaptation on contrast sensitivity

We have previously found that preferred adaptation reduces the contrast sensitivity or gain of MT cells, manifested as a change in the range of contrasts that evoke a response, but that it has little effect on responsivity (or response gain)[29]. To determine how flank adaptation affects the contrast and response gain of MT neurons to targets moving in the adapted direction and in a direction on the opposite, unadapted flank, we measured the response to stimuli of varying contrast (Methods) moving in either of these two directions before and after flank adaptation.

The population contrast response function for targets moving in the adapted flank direction, obtained by averaging the response of 11 cells after normalizing each to its preadaptation response to the full-contrast stimulus, showed that the sensitivity to low-contrast targets was reduced, whereas the response to full-contrast stimuli was unchanged (**Fig. 4a**). Thus, the maintained response observed in the adapted direction in our direction-tuning experiments does not indicate that flank adaptation has no effect on the response to stimuli moving in that direction. In the unadapted direction, contrast sensitivity was similarly reduced after adaptation: the minimal contrast capable of raising the firing rate above the spontaneous level increased from roughly 0.03 to more than 0.10 (**Fig. 4b**). Unlike the effect observed on the adapted flank, however, the maximal firing rate evoked by high-contrast stimuli moving in the unadapted direction was strongly reduced.

To compare the responsivity on the unadapted and adapted flanks, we calculated response ratios (the postadaptation response on the unadapted flank relative to that on the adapted flank) at each contrast level that evoked a measurable response. These ratios were 0.31, 0.29, 0.32 and 0.55 for contrasts of 1, 0.5. 0.25 and 0.125, respectively. Thus, the response on the adapted flank was two to three times stronger than that on the unadapted flank after adaptation, indicating that attractive shifts in direction preference occur at each of these test contrasts.

We conclude that flank adaptation reduces the contrast sensitivity for all test stimuli, and that attractive shifts in direction tuning are due to an additional reduction in response gain that occurs only for test stimuli that are different from the adapter.

Effect of adaptation on tuning in V1

Because most previous studies have reported that adaptation causes repulsive, not attractive, shifts of tuning in V1 (refs. 9–16), we recorded from V1 cells to determine whether our adaptation protocol induced shifts in V1 orientation tuning. We studied both direction-selective ($n = 22$) and non-direction-selective ($n = 18$) complex cells in nine macaque monkeys. We characterized direction-selective cells by the same methods used for MT. For non-direction-selective cells, we fitted von Mises functions to only the adapted lobe of the tuning curve.

An example of the effect of flank adaptation on a V1 direction-selective complex cell is shown in **Figure 5a**. Responsivity on both the adapted flank and opposite flank was reduced slightly, causing no shift in the preferred direction. The effect of flank adaptation on the preferred direction of our V1 population is shown in **Figure 5b**: non-direction-selective cells showed a small repulsive shift ($2.4 \pm 2.0°$; $P = 0.12$), whereas direction-selective cells showed a small attractive shift ($1.2 \pm 2.4°$; $P = 0.31$). There was a small difference between the two populations, but it was not statistically significant ($P = 0.14$). Although neither cell type showed significant changes in preferred direction on average, some individual cells did show reliable repulsive or attractive shifts.

The difference between the shift induced by flank adaptation in MT (attraction of 9.3°) and in V1 (repulsion of $0.4° \pm 1.6°$) was statistically significant ($P < 0.001$), as was the difference when the comparison was limited to direction-selective V1 neurons ($P = 0.003$). We conclude that our adaptation protocol shows a difference in the direction specificity of adaptation effects between MT and the V1 cells from which the MT is likely to receive input.

End-of-flank and null adaptation

To evaluate the range of adapted directions that induce attractive shifts in tuning, we adapted MT neurons with stimuli just outside the range capable of driving the cell ('end-of-flank' adaptation). On average, the adaptation direction in these experiments was 95° from the preferred direction and evoked a negligible mean response of 2.2 ± 2.0 ips ($n = 17$). For the cell shown in **Figure 6a**, adaptation at –93° had little effect on direction tuning. The population histograms confirm that end-of-flank adaptation had little effect on the preferred direction (**Fig. 6b**; mean shift: attraction of $0.7 \pm 1.8°$; $P = 0.69$), tuning bandwidth (**Fig. 6c**; mean ratio 1.07; $P = 0.20$) or responsivity of MT cells (**Fig. 6d**; mean ratio 0.98; $P = 0.35$). These results suggest that attractive shifts in tuning occur only for stimuli that lie within the tuning bandwidth of the cell.

MT cells are inhibited by motion in their null direction[29,31,32]. We and others have previously shown that null adaptation reduces the efficacy of this inhibition[29,33], and we therefore evaluated whether this reduction in inhibition affects the direction tuning of MT cells. For the cell shown in **Figure 6e**, null adaptation had little effect on direction tuning. On average, there was no change in the preferred direction (**Fig. 6f**; average attractive shift of $0.2 \pm 1.2°$; $P = 0.84$; $n = 22$; adaptation 135–225° from preferred) or responsivity (**Fig. 6g**; response ratio 0.97; $P = 0.28$) after null adaptation.

The direction-tuning bandwidth of some MT cells increased after null adaptation. This effect was not significant for the whole population (**Fig. 6h**; ratio of 1.04; $P = 0.16$; mean bandwidth increased from 81° to 86°), but when we considered only those cells that were suppressed below spontaneous firing by null motion, we found a significant broadening (ratio of 1.11; $P = 0.001$; $n = 16$). Finally, we evaluated whether the reduced efficacy of inhibitory input after null adaptation affected the response to a null stimulus and found that it was unchanged: the mean response to null motion was 1 ± 2 ips before adaptation and -2 ± 2 ips after ($P = 0.30$). We conclude that, although null adaptation reduces the efficacy of null or opponent inhibition[29], this has only modest effects on the direction tuning of most MT neurons.

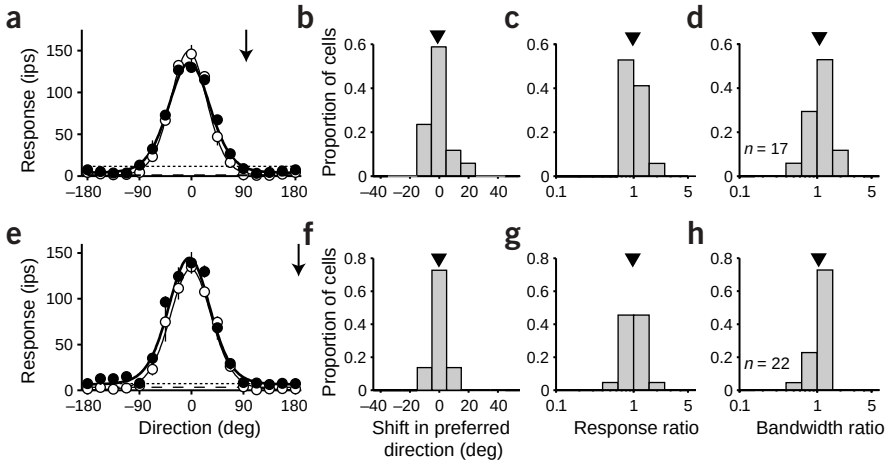

Figure 6 End-of-flank and null adaptation in MT cells. (**a**) Direction tuning before (○) and after (●) end-of-flank adaptation (direction indicated by arrow) for an MT cell. (**b–d**) Distributions ($n = 17$) show no change in preferred direction (**b**), tuning bandwidth (**c**) or responsivity (**d**) after end-of-flank adaptation. (**e**) Null adaptation has little effect on the direction tuning of a second cell. (**f–h**) Distributions ($n = 22$) of shifts in the preferred direction (**f**) and changes in responsivity (**g**) and tuning bandwidth (**h**) after null adaptation. Tuning bandwidth increases slightly after null adaptation, but preferred direction and responsivity are unaffected.

For convenient exposition, we divided the above data into categories according to the adapted direction (preferred, flank, end-of-flank and null). In reality, the adaptation direction differed from the preferred direction in a continuous manner. In **Figure 7**, we summarize the shifts in preferred direction and changes in tuning bandwidth as a function of the adapted direction for all cells. Attractive shifts in preferred direction are first apparent when the adapting direction deviates slightly from the preferred direction (10–20°), reach maximal strength for adaptation roughly 45° from the preferred direction, and are absent for adaptation greater than 90° from the preferred direction (**Fig. 7a**).

Considered individually, the shifts in direction preference were significant in roughly half of the cells (28 of 55); all but one of these shifts was attractive. In the remaining cells and across the population as a whole, there was a clear bias toward attraction when the adapting direction was between 15° and 75° from the preferred direction. Bandwidth was reduced most strongly when cells were adapted within 45° of the preferred direction (**Fig. 7b**; 17 of 22 preferred-adapted cells were individually significant), whereas adaptation at directions between orthogonal and null resulted in a slight increase in tuning bandwidth.

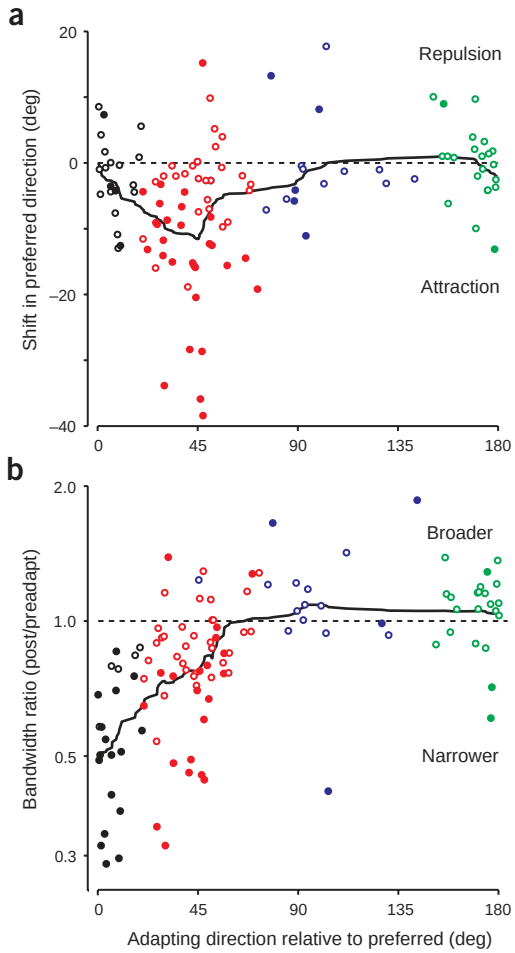

Figure 7 Changes in MT direction tuning as a function of adapting direction. (**a**) Shifts in preferred direction are shown for each cell. Preferred, flank, end-of-flank and null adaptation are colored black, red, blue and green, respectively. The black line shows a running average of the shift, calculated by averaging the neighboring ±10 data points. Filled symbols show cells for which the tuning shifts are significant ($P < 0.05$). (**b**) Bandwidth ratios as a function of the adaptation direction, represented as in **a**.

DISCUSSION

Most previous studies of neuronal adaptation to prolonged stimulation have been done in V1. In this structure, adaptation usually reduces neuronal sensitivity and responsiveness most for stimuli that are similar to the adapter, resulting in a postadaptation shift of tuning curves away from the adapter[9–16]. Our results in area MT show exactly the opposite effect: that is, prolonged adaptation to drifting sine-wave gratings reduces the responsivity of MT neurons least when the direction of the test stimulus is similar to the adapted direction. As a result, preferred adaptation causes a narrowing of direction-tuning bandwidth, whereas flank adaptation causes both a narrowing and a shift in tuning toward the adapted direction. The only other similar result of which we are aware comes from a preliminary report on the effect of adaptation on speed tuning in area MT of the awake monkey, where responsivity is reduced least when the speed of the test stimulus is matched to the adapter (B. Krekelberg, personal communication). Clearly, adaptation in MT produces effects unlike those that have been previously documented in V1.

We thought that it was important to compare directly our MT effects with effects in V1. In particular, we wanted to ensure that our MT results were not due to our experimental protocol and to compare our MT data with a sample of V1 cells enriched with

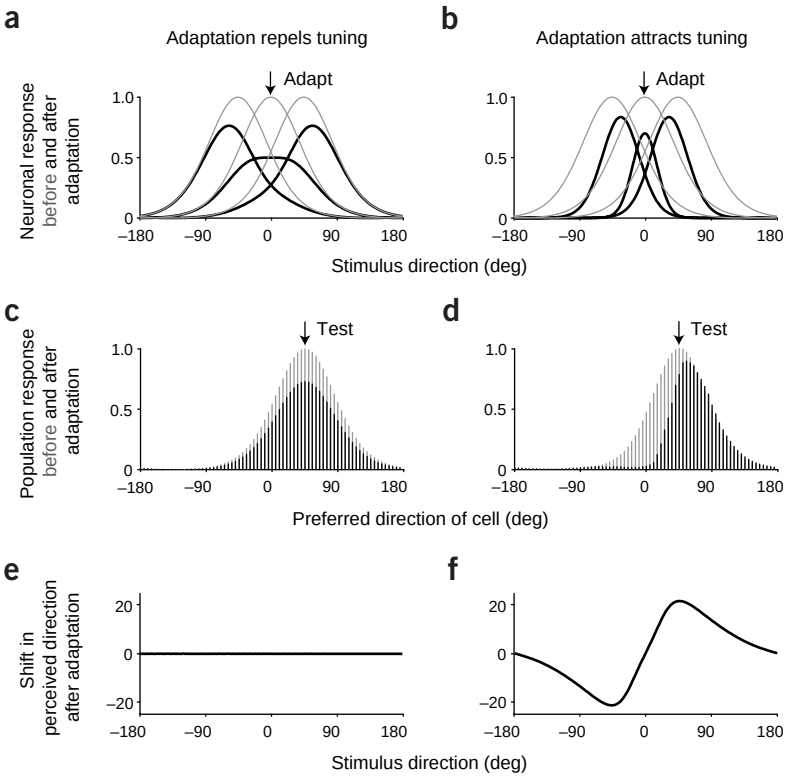

Figure 8 Changes in MT direction tuning after adaptation are consistent with perceptual effects. (**a**,**b**) Examples of tuning of model cells before (gray) and after (black) adaptation for two adaptation schemes: 'adaptation repels tuning' (repulsion, **a**) and 'adaptation attracts tuning' (attraction, **b**). Arrow indicates the adapted direction. (**c**,**d**) Population activity evoked by a test stimulus at 45° (indicated by arrow) for each adaptation scheme. Repulsion causes a reduction in activity but no shift in its distribution. Attraction results in both a reduced response and a shift in the distribution of activity 'away' from the adapting direction. (**e**,**f**) Shifts in population response for a range of test directions. Attraction, but not repulsion, gives rise to repulsive shifts in perceived direction similar to those observed psychophysically.

direction-selective complex cells—the cells that provide input to MT from V1 (ref. 34). We confirmed that the effects of adaptation on direction tuning in MT cells differ from those in complex V1 cells. The primary effect of adaptation on our V1 cells was to reduce neuronal responsivity with little change in preferred direction. We are therefore confident that the effects that we observed in MT cells do not arise from previously undetected properties of the subset of V1 cells that relay directional motion signals.

Although our V1 data do not show the significant repulsive tuning shifts previously reported in some studies[12–15], our cell sample was relatively small and we could easily have failed to detect a small shift in population tuning. Our V1 results are also in good agreement with those of a study[16] using a similar experimental design. That study found repulsive shifts in V1 orientation tuning only for cells in orientation 'pinwheels', and elsewhere in V1 adaptation decreased responsivity without changing tuning. Because most V1 neurons are outside pinwheels, the main effect of adaptation in V1 may be to reduce responses, with only a fraction of cells undergoing repulsive shifts in preferred orientation.

Potential mechanisms

Our previous finding that changes in MT neuronal contrast sensitivity are spatially specific led us to suggest that adaptation effects in MT are likely to be inherited from V1 neurons[29] because they have small receptive fields, are known to undergo changes in contrast sensitivity[35,36] and provide substantial input to MT[37]. The spatial specificity of adaptation in MT is not consistent with a substantial hyperpolarization of neurons after adaptation, as has been observed in cat V1 (refs. 38,39), and it seems to rule out other mechanisms that globally alter the responsivity of an adapted MT cell.

One explanation for the effect of adaptation on MT direction tuning is that it involves a change in the relative strength of excitation and inhibition received by adapted MT cells. Another study has evaluated the consequences of altering the strength of recurrent excitation and inhibition in a model of V1 orientation selectivity[40]. Recurrent connections in that model have a 'Mexican-hat' configuration, such that each cell receives excitation from cells with similar preferences and inhibition from cells with remote preferences. When adaptation is implemented as a reduction in the strength of recurrent excitation to cells driven most strongly by the adapter, the responsivity of these preferred-adapted cells decreases slightly and their tuning bandwidth decreases substantially, owing to maintained inhibition from remote cells. For flank-adapted cells, the loss of recurrent excitation causes a reduction in the response to all test stimuli, but the loss of lateral inhibition from neighboring (preferred-adapted) cells offsets this effect on the adapted flank. The net result is a slight decrease in tuning bandwidth and a shift in preference toward the adapted orientation, as we observed here in MT. In essence, the model involves competition among cells via lateral inhibition. Cells that lose excitation are disadvantaged in this competition, enabling neurons with offset preferences to shift toward the region of reduced excitation.

Although this model mimics the effect of adaptation on MT tuning, it relies on adaptation-induced alterations in recurrent circuitry. This seems inconsistent with our previous findings that adaptation in MT is due to weakened feedforward input[29], but a simple explanation could be that there is a stronger reduction in the feedforward input to cells contributing to recurrent excitation than to those providing recurrent inhibition. This could occur if the weakened feedforward input involved synaptic depression that is stronger for excitatory than for inhibitory cells, a suggestion that is supported by *in vitro* studies[41]. The basic behavior of the model can be also achieved by maintaining the strength of recurrent connections and by reducing most the strength of feedforward excitation to the cells tuned to the adapted direction.

Notably, with this implementation of the model, we would predict that stimuli that fail to adapt V1 cells strongly will also fail to give rise to attractive shifts in MT tuning. Preliminary experiments using prolonged adaptation with coherent dots support this prediction: adaptation with dots reduces the responsivity of MT cells but has little effect on direction-tuning bandwidth or preferred direction (A.K. and J.A.M., unpublished data). We have implemented these simple

variants of the model and found that they can produce tuning changes that are in qualitative agreement with our data. It is important to note, however, that the model relies on the assumption that the feedforward input to MT is broadly tuned and then sharpened by recurrent connections in MT. If the pool of neurons providing feedforward input to MT is selective, as suggested by antidromic stimulation experiments[34], then a different explanation will be needed.

Implications for perception

Adaptation causes the perceived direction of subsequently viewed stimuli to shift away from the adapted direction, the 'direction aftereffect' (DAE)[2,6–8]. A similar repulsive shift in perceived orientation, the 'tilt aftereffect' (TAE), has been studied extensively [1,2]. To test whether the adaptation effects that we observed in MT are consistent with repulsive shifts in perceived direction, we made a labeled-line model that computes perceived direction as the vector sum of the responses of the model cells, where the 'label' of each cell is its preferred direction before adaptation and the weight of each cell is given by the magnitude of its response. We chose this simple framework because it is intuitive and has been used previously to explore the perceptual consequence of changes in neuronal tuning and responsivity[2,17,19].

Consider two schemes: first, adaptation reduces responsivity for each cell most strongly for stimuli that are similar to the adaptation stimulus, as is often reported for cells in V1 ('repulsion'); and second, adaptation alters tuning in the manner that we observe in MT ('attraction'). The tuning of model neurons before and after adaptation at 0° is shown for each scheme, along with the distributions of activity in the population evoked by a test stimulus at +45° (**Fig. 8a–d**). The activity histograms are constructed by plotting the response of each cell to the test stimulus before and after adaptation.

In our particular simulation of repulsive shifts in tuning (**Fig. 8c**), adaptation reduces the population response but it does not alter its distribution. This is because repulsion is achieved by scaling the response to each test direction of each cell by a common value (Methods). By contrast, attractive shifts in tuning (**Fig. 8d**) cause the distribution of activity to shift away from the adapted direction by more than 20°. The main reason for this is that cells with preadaptation preferred directions in the range 15–45° shift their tuning toward the adapted direction and 'away' from the test direction, thereby reducing their response to the test stimulus; cells with preferred directions in the range 45–75° also shift their tuning toward the adapted direction, which in this case is also toward the test direction, thereby preserving their responses to the test stimulus. The effect is enhanced by the narrowing of the tuning curves of cells with preferred directions near 0°, which sharply reduces their response to the test stimulus.

The shift in the population vector, the model's measure of perceived direction, is shown for a range of test directions (**Fig. 8e**,**f**). Our particular simulation of repulsive shifts in tuning (**Fig. 8a**) predicts that there will be no change in the perceived direction of any test stimulus (**Fig. 8e**). By contrast, attractive tuning shifts (**Fig. 8f**) result in robust repulsive perceptual shifts, as has been found psychophysically[8].

The simulation shown in **Figure 8** reflects one possible implementation of repulsive shifts in tuning, but its main features are evident in a wide range of simulations that vary the degree to which the preferred direction is repelled or attracted, the tuning bandwidth is altered, and the responsivity is scaled after adaptation. The perceptual distortions predicted by simulations in which these factors were varied parametrically are shown in **Supplementary Figure 1** online. The results show that attractive shifts in tuning are not required for repulsive perceptual effects: if adaptation reduces responsivity enough, this alone can produce perceptual repulsion. The effect of reduced responsivity is enhanced when it is accompanied by attractive shifts and bandwidth narrowing, and it is weakened when tuning is repelled.

A similar conclusion has been reached in a model of the TAE: strong adaptation-induced losses in V1 responsivity can overcome the perceptual attraction predicted from repulsive tuning shifts alone (D.J. Jin *et al.*, *Soc. Neurosci. Abstr.* **29**, 266.11, 2003; see also ref. 19). In MT, however, the postadaptation reduction in responsivity is relatively modest, and the attractive shifts in tuning and the reduction in tuning bandwidth are of the form and magnitude needed to account for the DAE (which is roughly an order of magnitude larger than the TAE).

One might ask whether our experiments on anesthetized monkeys bear directly on perceptual aftereffects measured in alert humans. Opiate anesthesia of the type that we use seems to have little effect on the response or adaptation properties of MT neurons: both visual responses and adaptation are very similar in recordings from alert and anesthetized animals[42–44]. In addition, in human subjects, neither attention nor even visual awareness is required for the creation of visual aftereffects[45–47], although attention can modulate the magnitude of measured effects. We conclude that our results are likely to be accurate replicas of the neuronal effects in both alert monkeys and humans.

Finally, it is worth noting that the effects of adaptation in MT predict changes in both the perceived direction of a drifting stimulus (the DAE) and the apparent motion of a static or motion-balanced stimulus (the 'motion aftereffect'; MAE). Previously, we found that specific types of MAE could be explained by a postadaptation imbalance in the sensitivity of MT neurons tuned to opposite directions of motion[29], a suggestion that is consistent with our finding that preferred adaptation reduces the responsivity of MT neurons, whereas null adaptation has little effect on response. Null adaptation does, however, reduce the effectiveness of inhibition elicited by null-direction stimuli and thereby contributes to the MAE observed with compound stimuli composed of preferred and null drifting gratings. The DAE does not involve a direct comparison between preferred and null-adapted cells or a change in the strength of null inhibition. Rather, it arises primarily from shifts in preference and changes in the tuning bandwidth of cells with preferred directions at and near the adapted direction.

Conclusion

In summary, we have identified an effect of adaptation in MT that is different from any previously documented effect in V1. Rather than repelling the direction tuning of MT cells, adaptation attracts their tuning by a preferential reduction in responsivity for stimuli that are different from the adapter. A simple population coding model shows that the way in which adaptation alters MT direction tuning can readily predict the large repulsive shifts in perceived direction that are seen psychophysically. Tuning changes of the type previously observed in V1, by contrast, would produce little perceptual distortion, suggesting that the perceptual DAE is likely to arise from changes in MT or other areas downstream of V1. In addition to resolving discrepancies between neurophysiological and psychophysical effects, our data show that current theories[20–23] and mechanistic explanations[38,39,48] for adaptation observed in V1 convey only a partial picture of the way in which cortex adjusts to variations in sensory input.

METHODS

Recordings. We recorded from ten cynomolgus (*Macaca fascicularis*), one bonnet (*M. radiatum*) and one pig-tailed (*M. nemestrina*) adult male monkeys. The procedures used in our laboratory for single-unit recording in anes-

thetized (sufentanil citrate, 4–8 μg per kilogram (body weight) per hour), paralyzed (vecuronium bromide, 0.1 mg per kilogram per hour) macaque monkeys have been described in detail[49]. All experimental procedures were approved by the New York University Animal Welfare Committee.

MT recordings were made with platinum-tungsten or tungsten-in-glass microelectrodes through a craniotomy centered 16 mm lateral to the midline and 2 mm posterior to the lunate sulcus; electrode penetrations were made at an angle of 20° from horizontal. V1 recordings were made in the operculum (where the receptive fields were within 5° of the fovea) and calcarine sulcus (within 12–18° of the fovea), with vertical penetrations roughly 10 mm lateral to the midline and 4–10 mm posterior to the lunate sulcus. Signals from the microelectrode were amplified, bandpass-filtered (300 Hz to 10 kHz) and fed into a hardware discriminator (Bak Electronics). Spike times were saved with a temporal resolution of 0.25 ms. We made electrolytic lesions (2 μA for 5 s) at the end of each recording tract and used published methods[29] for histological confirmation of the recording sites.

Visual stimuli. Stimuli were luminance-modulated, drifting sine-wave gratings presented at a frame rate of 100 Hz by using a 10-bit Silicon Graphics board operating at a resolution of 1,024 × 731 pixels. The monitor (Eizo T550) subtended about 22° of visual angle and had a mean luminance of roughly 33 cd/m^2. For each cell, we determined, in this order, the optimal direction, spatial and temporal frequency, position and size of a drifting sine-wave grating. Full-contrast gratings were presented to the dominant eye in a circular aperture, surrounded by a gray field of average luminance. Stimuli were presented in the classical receptive field, which was defined as the smallest stimulus size that evoked a response no less than 95% of the maximal response[49], and did not extend into the receptive field surround.

We used two different protocols in our adaptation experiments. In the first adaptation protocol, a trial consisted of a single randomized sequence of 1-s test stimuli (16 directions spanning 360° in 22.5° steps), followed by a 40-s adapting stimulus and a second sequence of test stimuli, each preceded by a 5-s top-up stimulus. Each 'test–adapt–test/top-up' trial was followed by at least 3 min of recovery (**Fig. 1**). We recorded three to five trials for each adaptation direction, block-randomizing the presentation of each direction. In the second adaptation protocol, we ran several sequences of test stimuli before and after adaptation, with a single recovery period (~15 min) between adaptation conditions. We obtained similar results with the two protocols and pooled the results. In experiments evaluating the effect of adaptation on contrast sensitivity, we used the same experimental design and recorded responses to seven test stimuli spaced in equal logarithmic contrast steps between 0.016 and 1.0, presented in a randomized sequence. Spontaneous activity in all experiments was measured either by using a blank stimulus interleaved with the test stimuli or during a brief epoch immediately preceding and following the stimulus sequence.

Data analysis. We characterized direction tuning, both before and after adaptation, by fitting the von Mises function (a circular approximation to the gaussian function) to the mean response using the χ^2 minimization algorithm STEPIT[50]. The von Mises function is

$$ae^{b\cos(\theta - x_c)} + m$$

where a scales the height of the tuning curve, b determines the tuning bandwidth, x_c is the location of the tuning curve peak, θ is the direction and m is the spontaneous firing rate of the cell. Negative responses in the model were set to zero. Because changes in the parameter b also affect the height of the curve, we report alternative bandwidth and responsivity metrics extracted from the fits.

We removed 5 cells (of 71) from the data set that were poorly tuned and thus not well fitted by the von Mises function. In the remaining data set, the fits accounted for 92% of the variance in the data. We used bootstrap analysis to evaluate the significance of changes in tuning in individual cells. Specifically, for each cell we combined all trials of pre- and postadaptation data. We then created 500 'preadapt' and 'postadapt' data sets by choosing random subsets of the data with replacement. We fitted each of these 500 data sets in the same way that we fitted the measured responses. Statistical significance was determined by the rank of the measured values in the set of bootstrap fits.

All indications of variation in the graphs and text are standard errors of the mean (s.e.m.). The statistical significance of all results was evaluated with t-tests.

Simulations. To simulate the perceptual effects of adaptation, we used a labeled-line model consisting of 720 cells, spanning 360° in 0.5° increments, with the maximum response of each cell set to 1 and with a tuning bandwidth matching the average for our MT population.

In the first scheme ('repulsion'), adaptation reduced the response of each cell most strongly in the adapted direction. We implemented this effect by multiplying the tuning of each cell by an inverted gaussian function (standard deviation, s.d., 83°) whose minimum (0.5) lay in the adapted direction and whose value was ~1 for directions located 2 s.d. away from the adapted direction. We chose the shape and minimum value of this function so that the changes in tuning observed after flank adaptation would approximate those previously reported in V1 (refs. 12–15). Specifically, peak responsivity was reduced most strongly in cells that were best matched to the adapter, and the preferred direction of flank adapted cells shifted away from the adapter.

In the second scheme ('attraction'), we modeled the effect of the adaptation in MT by using the measured shifts in preferred direction and changes in tuning bandwidth and responsivity. We obtained similar predicted perceptual effects in the model when the population response was read out by a 'winner-takes-all' rule or by maximum likelihood estimation (by fitting a von Mises template to the response).

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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