Motion Adaptation in Area MT

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van Wezel, Richard J. A. and Kenneth H. Britten. Motion adaptation in area MT. *J Neurophysiol* 88: 3469–3476, 2002. 10.1152/jn.00276.2002. In many sensory systems, exposure to a prolonged stimulus causes adaptation, which tends to reduce neural responses to subsequent stimuli. Such effects are usually stimulus-specific, making adaptation a powerful probe into information processing. We used dynamic random dot kinematograms to test the magnitude and selectivity of adaptation effects in the middle temporal area (MT) and to compare them to effects on human motion discrimination. After 3 s of adaptation to a random dot pattern moving in the preferred direction, MT neuronal responses to subsequent test patterns were reduced by 26% on average compared with adaptation to a static pattern. This reduction in response magnitude was largely independent of what test stimulus was presented. However, adaptation in the opposite direction changed responses less often and very inconsistently. Therefore motion adaptation systematically and profoundly affects the neurons in MT representing the adapted direction, but much less those representing the opposite direction. In human psychophysical experiments, such adapting stimuli affected direction discrimination, biasing choices away from the adaptation direction. The magnitude of this perceptual shift was consistent with the magnitude of the changes seen in area MT, if one assumes that a motion comparison step occurs after MT.

INTRODUCTION

The middle temporal area (MT or V5) of primate extrastriate cortex is heavily involved in motion perception, according to many studies (for review, see Albright and Stoner 1995). In perceptual studies of motion processing, adaptation has been a very revealing tool. However, adaptation has been little studied in MT. In this study, we combine motion adaptation with dynamic random dot test stimuli to quantitatively assess the specificity and magnitude of adaptation-induced changes in the response of single MT neurons.

Perceptual studies of motion adaptation are numerous, in part because of the remarkable salience of the well-known motion aftereffect (MAE; for review, see Mather et al. 1998). After prolonged viewing of a pattern moving in one direction, a subsequent stationary pattern is perceived to move in the opposite direction. What is interesting about this phenomenon is the *positive* percept of motion, because most perceptual adaptation effects are negative (i.e., selective reduction in sensitivity to the adapting stimulus). Two classes of models have been proposed to account for this property of the MAE. First, mutual inhibition among neurons tuned for different

directions of motion might be responsible (e.g., Cornsweet 1970). According to this model, adaptation would attenuate the responses of neurons tuned to the adaptation direction, which would disinhibit neurons tuned to the opposite direction, leading to enhanced activity and the perception of motion. On the other hand, even without such mutual inhibition, the MAE might result from selective loss of activity of neurons representing the adaptation direction (Mather 1980). In this model, no neurons are active above baseline following adaptation.

Dynamic random-dot kinematograms, in which the motion coherence can be varied, are commonly used stimuli to explore motion processing mechanisms. These stimuli have been used for both psychophysical (e.g., Barlow and Tripathy 1997; Morgan and Ward 1980) and physiological studies (e.g., Britten et al. 1992; Celebrini and Newsome 1994). They are particularly useful for the present purposes because they allow quantification of the magnitude of motion adaptation effects (Blake and Hiris 1993). This application rests on the fact that there is a smooth stimulus gradient from strong motion in one direction through neutral (incoherent or pure noise) stimuli to strong motion in the other direction. Biases such as those induced by motion adaptation result in systematic shifts of perception along this axis and can be conveniently quantified in physical stimulus units.

In our experiments, we preceded test stimuli with one of three types of adapting stimuli: stationary or two opposite directions. We then tested either perceptual or MT responses to subsequently presented test stimuli that varied along the continuum of motion just described. We found that MT neuronal responses were systematically depressed following adaptation in their preferred direction, but not systematically affected by adaptation in the direction opposite their preferred direction. The effects of adaptation could be considered as a horizontal shift on the stimulus axis; the magnitude of this shift was comparable to that seen in perception. The results of this experiment have appeared as an abstract (Britten and van Wezel 1998).

METHODS

Preparation and recordings

We recorded single MT cells in three adult female rhesus monkeys (*Macaca mulatta*). Before recording, each monkey had been trained to fixate a stationary red spot of 0.23° diam in the presence of visual

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stimuli. The animal's fluid intake was restricted, and behavioral control was achieved using operant conditioning techniques. The animal received a fluid reward (a drop of water or juice) for keeping its eyes within a window (1–2.5° width) surrounding the fixation point for the duration of the trial. All surgical and experimental methods followed previously described procedures (Britten et al. 1992), conformed to the National Institutes of Health Guide for the Care and Use of Laboratory Animals, and were approved by the UC Davis Animal Care and Use Committee. Under deep surgical anesthesia, each animal was implanted with a scleral search coil (Judge et al. 1980) and was equipped with a stainless steel head restraint post and recording cylinder (Crist Instrument, Damascus, MD) located over the occipital cortex. The monkeys were given at least 2 weeks to recover from surgery before recording.

A plastic grid secured inside the cylinder provided a coordinate system of guide tube support holes at 1-mm intervals (Crist et al. 1988). Guide tubes were inserted transdurally through these holes, with local anesthetic if necessary. Parylene-insulated tungsten microelectrodes (MicroProbe, Potomac, MD) were inserted through these guide tubes, and neural signals from these electrodes were amplified, filtered, and displayed by standard methods. Spikes were isolated using a time-amplitude window discriminator (Bak Electronics, Germantown, MD) and converted to voltage pulses that were fed to the computer controlling the experiment. Data acquisition and experimental control were managed by the software package REX (Hays et al. 1982). Neurons were determined to be located in MT by physiological criteria: receptive field size, directionally selective responses, columnar organization for preferred directions, and appropriate retinotopic organization (Albright et al. 1984; Maunsell and Van Essen 1983b; Zeki 1974). In two monkeys, we verified histologically that the recording region corresponded to the heavily myelinated zone on the posterior bank of the superior temporal sulcus (STS). This landmark is a very reliable indicator of the location of MT (Desimone and Ungerleider 1986; Maunsell and Van Essen 1983a). This verification is not yet available for the third monkey because it is currently involved in other experiments.

Once a single unit was isolated, the receptive field was mapped using hand-controlled stimuli, typically moving bars of light. We only included in our analysis cells that were fully directionally selective, by which we mean that there is no overlap in the response distributions for the preferred and null directions at the highest coherence tested (Britten et al. 1992). This criterion need not imply a DSI [the standard index of directionality, calculated as (pref − null)/(pref + null)] near 1.0, nor that the cells be silent in their null direction. Thirteen of 87 cells did not meet this criterion. We imposed this criterion only for consistency with previous work, but inspection of the excluded cells' data showed that the adaptation effects were very similar as that from the retained cells (data not shown).

Stimuli

We used an adaptation-test paradigm similar in concept to ones used in human psychophysical studies of motion perception (Blake and Hiris 1993; Lankheet and Verstraten 1995; Raymond and Braddick 1996). The dynamic random dot stimulus we employed is similar to the ones used by Newsome and colleagues (Britten et al. 1992). A field of randomly positioned white dots (Fig. 1A) on a dark background was presented in a circular aperture on a color monitor (Mitsubishi DiamondPro 21, 1280 × 1024-pixel resolution, 72-Hz frame rate). Dot luminance was 60 cd/m² on a background <1 cd/m², and the screen distance was 57 cm. The random dot pattern was matched to the dimensions of the classical receptive field of an isolated MT neuron. The dot speed was adjusted to the cell's preferred speed. Dots were 0.18° in diameter, and dot density was 2.8 dots/sq. deg on average. See Fig. 1B for timing of events in a single trial. During the 3-s adaptation phase, all dots moved in the same direction (100% coherence) or were stationary. During the 1-s test phase that
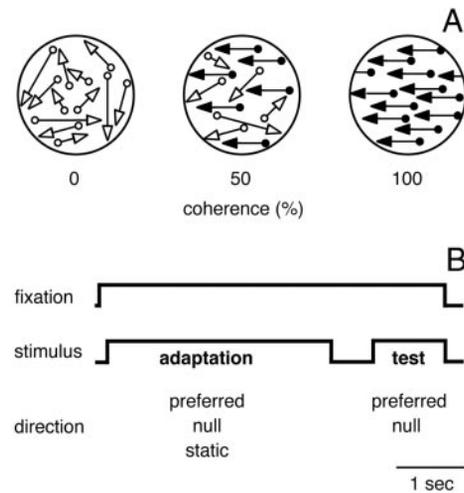

FIG. 1. Experimental design. A: visual stimuli consisted of a pattern of randomly placed white dots on a black background. Each dot was replotted either with a specific step size and in a specific direction (filled symbols) or at a random location (open symbols). Independent probability for each dot to be displaced coherently is what we define as the percentage coherence and determines the signal strength in the display. B: trial started when the monkey fixated a red dot on the screen. After 250 ms, a coherent adapting dot pattern was presented for 3 s, either stationary or moving in the preferred or opposite (null) direction. After adaptation, the screen was blank for 0.5 s. Following the blank period, the cell's directional sensitivity was assessed by presenting random dot patterns at different coherence levels moving in either the preferred or null direction for 1 s.

followed, the stimulus motion content was varied by changing the percentage of dots moving coherently, while the remaining dots appeared briefly at random locations. At 0% coherence, this results in a dynamic noise pattern, with no net motion direction. As a convention, we use negative coherence values for motion opposite to the cell's preferred direction. Typically, we presented six to seven coherence levels in each direction, including 0% and 100% coherence. All directions and coherence levels during the test period were pseudorandomly chosen and repeated ≥7 times. The coherence levels were log spaced, and the range was adjusted for each cell separately, depending on the cell's sensitivity to moving random dots. We presented combinations of the three adaptation conditions (preferred, null, and static), both test stimulus directions, and all coherence values in a fully counterbalanced design. Adaptation conditions were either pseudorandomly ordered or in a fixed sequence. We found no significant differences in our results between those two paradigms (t-tests, df = (18,56), all P > 0.05), so the data were pooled for analysis. Trials in which the monkey broke fixation were discarded.

Human psychophysics

Subjects were comfortably seated facing the screen, used a chin rest for head stabilization, and were instructed to maintain fixation during trials. Stimulus conditions and timing were the same as in the monkey physiological experiments (Fig. 1). After a trial, the subject pressed a button to indicate the perceived direction of motion during the test phase. The stimulus parameters were similar to those used on average in the MT recordings. The random dot pattern was always 10° in diameter at an eccentricity of 10°, moving at a speed of 20°/s along a horizontal axis of motion.

Data analysis

Coherence-response functions for each adaptation and each test condition were fitted with linear functions to calculate the intercept and slope. Because slopes of such functions often differed in the
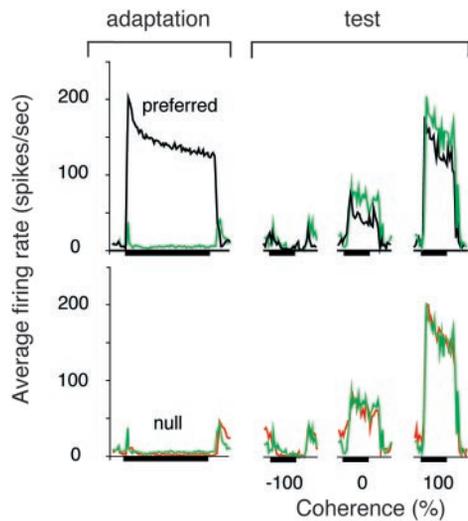
FIG. 2. Effect of motion adaptation on middle temporal (MT) cell responses. Peristimulus time histograms from a single MT cell during the adaptation (*left*) and 3 test conditions (from *left* to *right*: null direction 100% coherence, 0% coherence, and preferred direction 100% coherence). The black line (*top*) shows the histogram resulting from adaptation in the preferred direction, and the red line (*bottom*) shows the response after null direction adaptation. In both panels, the green line shows the histogram for the static control condition. Solid bar beneath each histogram indicates the duration of the visual stimulus.

preferred and null directions, we fit separate lines to each. Thus for any single adaptation condition, the most elaborate fit would include four parameters (2 slopes and 2 intercepts). For the full dataset for a single cell, we would thus employ 12 free parameters. To evaluate the effect of adaptation for each cell, we would remove parameters from this full model, testing whether each removed parameter caused a significant worsening of the overall likelihood of the model fit. For example, to evaluate the effects of preferred direction adaptation on the intercept of the coherence-response function to preferred direction stimuli, we would compare two fits to these data: either two lines with a single intercept (3 parameters) or two lines with two intercepts (4 parameters). The model with more parameters would always perform better, of course, but to evaluate how much better it performed, we used a nested likelihood ratio test. The difference in log likelihoods from the two fits is approximately χ^2 distributed, and this difference was tested against a critical value corresponding to $\alpha = 0.05$ (Hoel et al. 1971), derived under the null hypothesis that the two datasets actually shared a single intercept. This same procedure was used to isolate and test the effects of adaptation for each parameter and each test condition.

Human psychophysical data and model predictions were fit by a cumulative Gaussian (probit) function of the form

$$P(\text{adap}) = \frac{1}{\sigma \sqrt{2\pi}} \int_{-\infty}^{-c} e^{\left(\frac{-(x-u)^2}{2\sigma^2}\right)} dx \qquad (1)$$

where $P(\text{adap})$ is the probability of a choice in the adaptation direction, c corresponds to coherence, μ specifies the coherence where $P(\text{adap}) = 0.5$ (mean of Gaussian), and σ specifies the slope of the function. All functions were fit using maximum likelihood estimation.

RESULTS

Physiological results

We isolated single MT neurons from three monkeys, mapped each cell's RF, and determined its preferred direction. We presented 100% coherence adapting stimuli moving in

either the preferred or opposite (null) direction for 3 s. As a reference condition, we used a contrast- and luminance-matched adapting stimulus (static condition), consisting of stationary random dots. Both adapting and test stimuli were matched to the cell's RF size, location, and preferred speed.

Only adaptation in the preferred direction affected the responses of most MT cells, and a representative example is shown in Fig. 2. In the *top row*, the adapting stimulus was in the preferred direction. In *both rows*, the green curve depicts the responses to the control trials, with a stationary adapting stimulus. Following adaptation in the preferred direction, for any test coherence level where there was a measurable response, this response was reduced following preferred direction adaptation. On the other hand, null direction adaptation (*bottom row*, red curves) did not noticeably affect the magnitudes of the responses. Adapted and control histograms appear superimposed throughout. Therefore to quantify the effects of adaptation, we averaged the responses over the test stimulus periods to produce full coherence-response functions as shown in Fig. 3.

Compared with the static reference condition (Fig. 3, green dashed lines, open circles), adaptation in the preferred direction (black lines, filled squares) reduced responses for both test directions and all coherence levels. Adaptation in the null direction (red lines, X symbols) did not affect the cell's response; the response functions of the reference and null direction adaptation condition superimpose and are hardly discernable. Linear fits (Britten et al. 1993) to these data provided estimates of intercept (response at 0% coherence) and slope for each of the six different adaptation and test conditions. Changes in intercept without changes in slope indicate that responses are affected equivalently for all test coherence con-
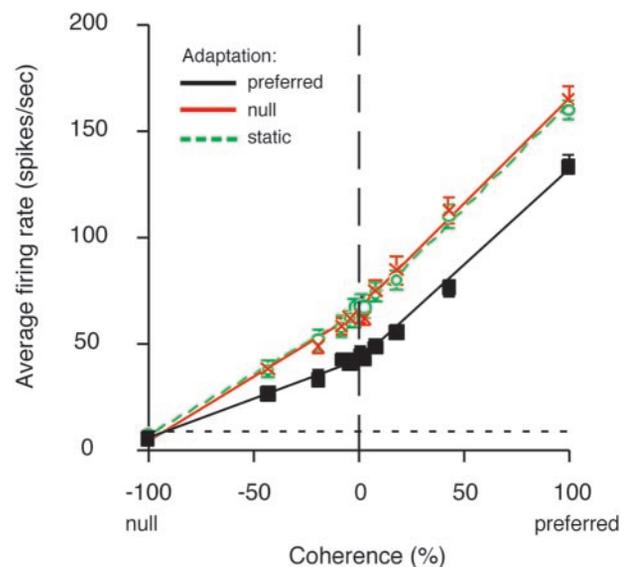

FIG. 3. Effect of motion adaptation on average MT cell activity. Average responses during the 1-s test stimulus presentation from a single MT cell. This is the same cell as presented in Fig. 2. Positive coherence levels denote preferred direction test stimuli; negative numbers show null direction. Color conventions as in Fig. 2. Adaptation in preferred direction, ■ and black line; adaptation in null direction, X and red line; adaptation with a static pattern, ○ and green dashed line. Note that the data points and linear fits of adaptation in the null direction and adaptation with a static pattern are hardly discernable. Error bars represent ±SE and the horizontal dashed line indicates spontaneous activity.
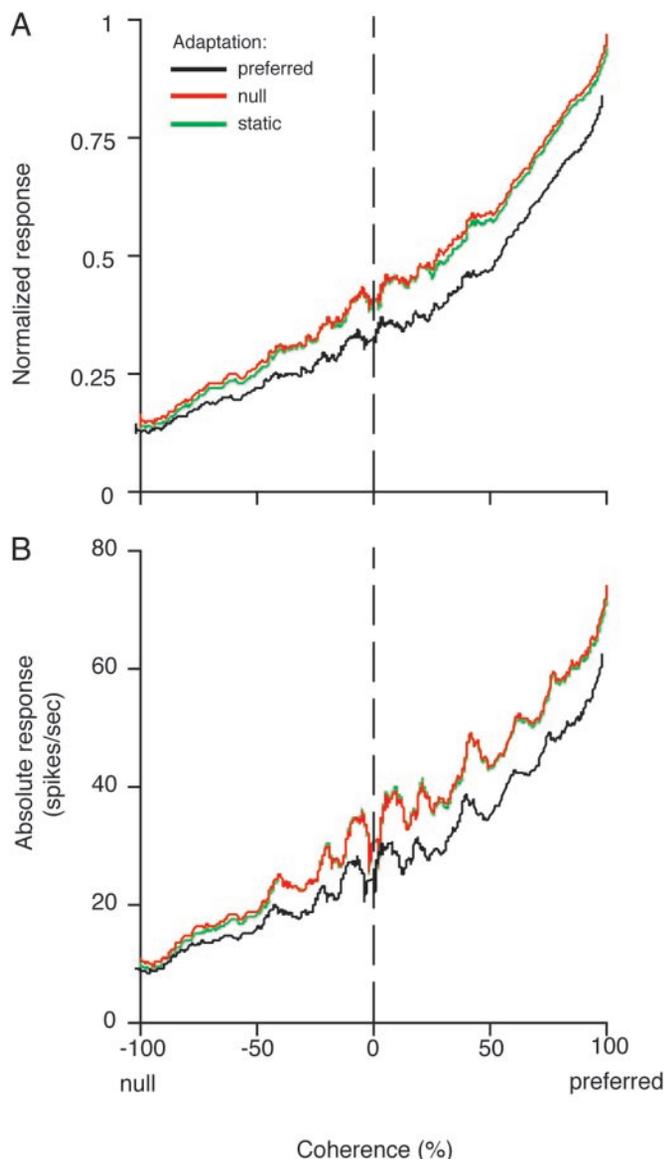
FIG. 4. Population response. Average response for 74 MT neurons during the 1-s test stimulus for the 3 different adaptation conditions. For each cell, individual responses were first normalized to the maximum response of the cell. Then all points were pooled, and a 100-point moving boxcar average was calculated to produce each smooth curve in the figure. This approach was necessary because the exact coherence values chosen differed from cell to cell. *A*: averages of normalized responses, giving each cell equal weight. *B*: averages of nonnormalized "raw" responses, which give each spike equal weight. Noise of the 3 curves is correlated because we tested different coherence values for each neuron, and some neurons have a higher or lower activity than others for all 3 adaptation conditions.

ditions, while slope changes reveal effects whose magnitudes depend systematically on the test coherence. For the example MT neuron in Fig. 3, the most apparent effect of adaptation in the preferred direction is a decrease in the intercept, although slope is also modestly reduced, especially for null direction test stimuli. Together, both changes substantially decreased neuronal response following adaptation in the preferred direction, but not after adaptation in the null direction.

The average response of all 74 neurons recorded (Fig. 4) was similar to the response of the example neuron in Figs. 2 and 3. In Fig. 4*A*, each neuron's response was normalized to its

maximum response across all conditions. Adaptation in the preferred direction substantially decreased the response (Fig. 4*A*, black line), while the response after adaptation in the null direction (red line) was hardly discernable from the responses in the static condition (green lines). In Fig. 4*B*, we show the nonnormalized version of the same analysis. The similarity of these curves to those in Fig. 4*A* shows that adaptation effects are similar, in their dependence on coherence, for both highly responsive and less-responsive neurons.

For each cell, we calculated the ratio of the intercept (Fig. 5, *A, B, E,* and *F*) and slope (Fig. 5, *C, D, G,* and *H*) under each adaptation condition to the same parameter under the static reference condition. Because separate functions were fit to preferred and null direction test stimuli, separate ratios were calculated for each test condition. Ratios of unity demonstrate that adaptation had no effect. After adaptation in the preferred direction (Fig. 5, *A–D*), most cells had ratios under 1, indicat-
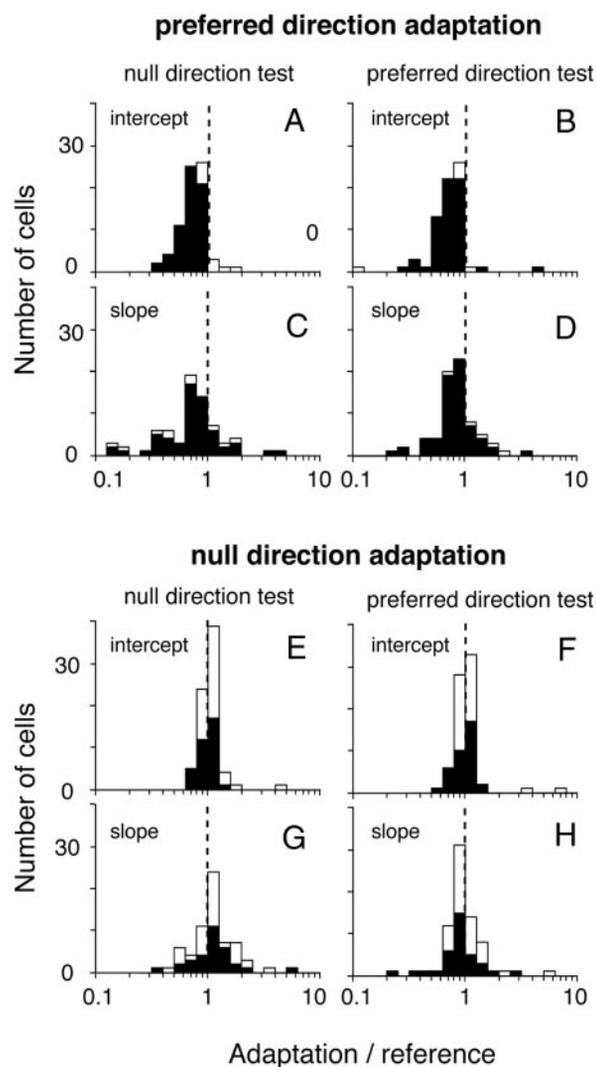

FIG. 5. Summary of adaptation effects on linear fit parameters. For each parameter, test condition, and adaptation condition, the ratio of adaptation over reference condition (adaptation with a static pattern) was calculated, and the distributions show the frequency of different ratio values in our sample of 74 cells. The vertical broken line in each graph indicates a ratio of 1.0, and filled bars indicate cells with a significant effect of motion adaptation. In cases where intercept or slope approached zero, the ratios became unstable and could fall outside the scale (*A–H*: 4, 1, 0, 2, 4, 2, 8, and 1 cells, respectively).

ing a decrease in intercept and slope compared with the reference condition. This decrease was highly significant for the intercept and slope (Wilcoxon signed-rank test, $P < 0.01$) for both test directions (Table 1). Overall, the coherence response functions of 89% of the cells were significantly changed by preferred direction adaptation, as indicated by the filled bars (nested log likelihood test, $P < 0.05$). The mean difference in intercept between adaptation with a static pattern and adaptation in the preferred direction was 26%.

By contrast, following null direction adaptation, the effects were much less pronounced and much less systematic. Fewer than one-half (47%) of these response functions were significantly affected by null direction adaptation. Furthermore, the sign of effects were more or less equally distributed, so that there was no significant change in intercept at the level of the whole sample (Wilcoxon signed-rank test, $P > 0.1$). This result is completely consistent with the less assumption-dependent population average analysis shown in Fig. 4, and the similarity of the two supports the assumptions in the linear analysis.

The summary data in Figs. 4 and 5 suggest that adaptation in the preferred direction caused more of a vertical shift than a slope change. While the effects on both intercept and slope were significant (Wilcoxon signed-rank test, $P < 0.01$), the effect on intercept was much more consistent in sign and magnitude. Furthermore, the effects on slope were larger when tested in the null direction (Table 1), which largely was a consequence of "floor effects." When tested in the preferred direction, where free of such artifacts, the magnitude of the slope changes were smaller than the effects on intercept. Similarly, when tested individually, effects on intercept were much more frequent than effects on slope. Of the neurons significantly affected by adaptation in any way, 96% showed significant changes in intercept (likelihood ratio test, $P < 0.05$). On the other hand, only 40% of the neurons showed significant changes in slope. All of this analysis taken together leads to the conclusion that the effects of adaptation are dominated by subtractive effects, which mostly manifest themselves as changes in the intercepts of neuronal response functions.

We were interested in exploring what aspects of the cells' responses predicted the magnitude of adaptation-induced shifts, and we address this in Fig. 6. In Fig. 6A, we explore whether the overall responsiveness of the cell predicts the
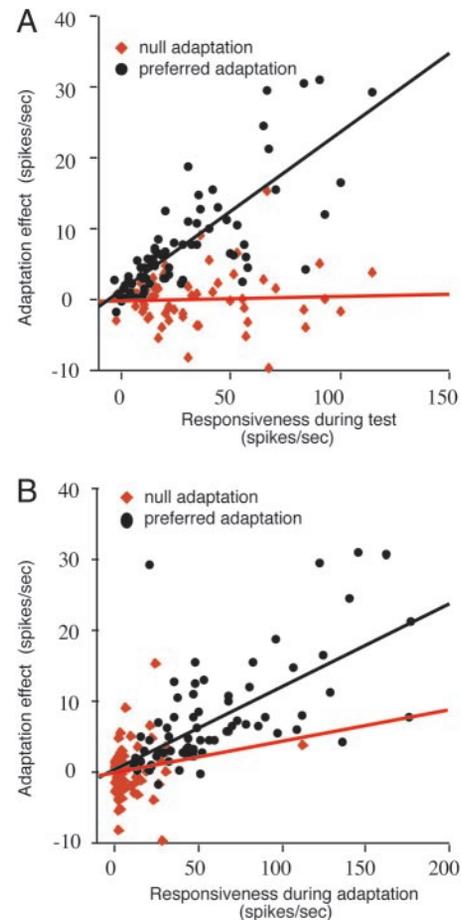

FIG. 6. Relationship between adaptation effects and cell responsiveness. For each direction of adaptation (black: preferred, red: null), we relate the magnitude of adaptation effect to 2 measures of the responsiveness of the cell. To characterize the effect of adaptation, we used the difference in intercepts between the adaptation state of interest and the static adaptation condition. *A*: responsiveness was expressed as the intercept of the linear fit after static adaptation. Linear regressions (color-matched lines) were as follows: preferred direction: $y = 0.76 + 0.23x$; null direction: $y = -0.22 + 0.01x$. *B*: responsiveness was expressed as the average activity during the adaptation period. Linear regressions: preferred direction: $y = 0.16 + 0.12x$; null direction: $y = -0.52 + 0.04x$.

magnitude of adaptation effect. We characterized the responsiveness of the cells by the intercept of their coherence-response functions (in essence, the response to 0% coherence stimuli). We find that for preferred direction adaptation, the responsiveness of the cell predicts quite accurately the magnitude of the adaptation ($r = 0.78$, $P < 0.001$). However, for null direction adaptation, adaptation effects are poorly predicted by the responsiveness of the cell ($r = 0.05$, $P > 0.5$). This analysis suggests, at least for preferred direction adaptation, that at the population level, adaptation effects scale with response in a manner consistent with a divisive mechanism. Additionally, this analysis suggests that there might be a difference between the mechanisms of preferred and null direction adaptation.

The effect of adaptation is also systematically related to the cells' responses to the adapting stimuli themselves, and this is illustrated in Fig. 6B. In this figure, we relate the effect of adaptation to the average firing rate of the cell during the 3-s adaptation period. Once again, for preferred direction adaptation, the adaptation is well predicted by the response to the

TABLE 1. *Linear fit parameter ratios*

	Preferred Direction Adaptation		Null Direction Adaptation	
	Mean Ratio	P Value	Mean Ratio	P Value
Intercept				
Preferred direction test	0.72	<0.01	1.01	0.80
Null direction test	0.77	<0.01	1.03	0.20
Slope				
Preferred direction test	0.82	<0.01	0.94	0.09
Null direction test	0.72	<0.01	1.09	0.01

The geometric mean of the ratio of linear fit parameters, intercept and slope, under each adaptation condition to the same parameter under stationary reference condition. The statistical significance of the difference from unity is calculated with a Wilcoxon signed rank test. Overall 89% of the cells was significantly changed by adaptation in the preferred direction and 49% by adaptation in the null direction (see METHODS).

adapting stimulus ($r = 0.58$, $P < 0.001$). For the null direction, the answer is less clear. There is no statistically reliable correlation between these two measures ($r = 0.17$, $P > 0.1$), but this might simply be a consequence of there being little response in the null direction, and little variance in this response across the sample of cells. There are some statistically reliable effects of null direction adaptation (see Fig. 5), but these do not appear to be related to the cells' responses to the adapting stimulus. However, to really address this question, adapting stimuli of intermediate effectiveness would be necessary.

In summary, our physiological results show that motion adaptation in one direction systematically reduces the response of neurons tuned to the same direction and affects the responses of oppositely tuned neurons much less systematically. Therefore we might expect performance on direction discrimination tasks also to be selectively affected by directional adaptation. To test this under our stimulus conditions, we performed a psychophysical adaptation experiment on human subjects. Ideally, of course, this experiment would have been performed in monkeys as well, but measuring perceptual illusions in nonhuman subjects is difficult. Monkeys are skillful at figuring out reward contingencies, and would not report their perceptions "honestly" if another strategy would bring them greater reward. After adaptation, they would certainly gain reward by counteracting the perceptual bias with a cognitive strategy. Because motion discrimination thresholds for our stimuli are similar in human and monkeys (Newsome and Paré 1988), we felt confident in avoiding this problem by testing human subjects instead.

Psychophysical results

We tested the perceptual effects of our adapting stimuli in human psychophysical experiments. Three subjects (2 of whom were unaware of the goals of the experiment) reported perceived motion direction under stimulus conditions that were chosen to match the average conditions in our physiological experiments. In these experiments, we assumed there would be no systematic effect of motion direction, so test and adaptation directions were always to either the left or the right (in the physiological experiments, the directions were matched to the cells' tuning). Three different adaptation conditions (left, right, and static) were randomly interleaved, so that the subjects' average adaptation state would be close to neutral. Subjects were instructed to faithfully report their percepts, irrespective of the adaptation direction, and avoid compensating for illusory motion. Full psychometric functions spanning a range of coherence levels were collected, under each of the three adaptation conditions. In Fig. 7, the effects of adaptation are shown by the difference between the curves with open circles (control) and those with solid squares (adapted). For these plots, the results of both adaptation directions have been combined for graphic clarity and plotted relative to the adaptation direction (positive coherence denotes motion in the adaptation direction). The effects of adaptation were well described as a simple horizontal shift of the psychometric function away from the adaptation direction. The average value of this shift across the three subjects was 17%. In addition, there was a modest reduction in the slopes of the psychometric functions for all three subjects, averaging 35%.
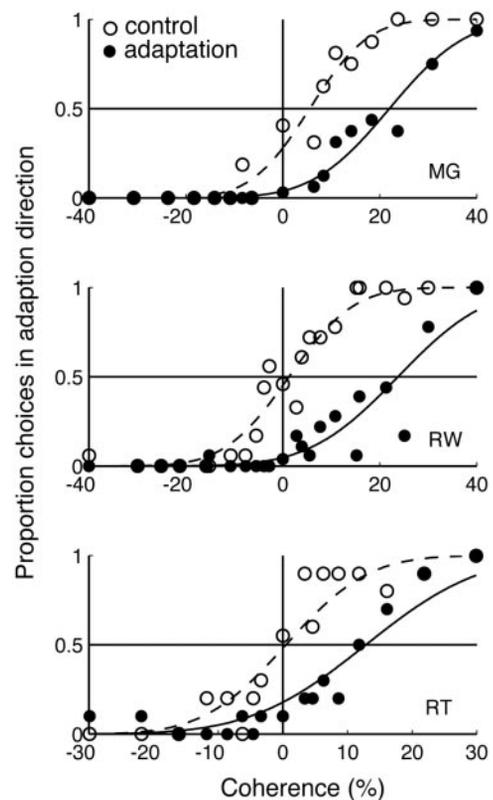

FIG. 7. Human psychophysics. Average results of decisions on motion direction during the test phase made by 3 human subjects. Subjects MG and RT were naive with respect to the goal of the experiment. The proportion of choices in favor of the adaptation direction is plotted against the coherence level during the test phase. The smooth curves though the data points were best-fit Probit functions (see METHODS), whose σ parameters estimate the steepness of these functions. The sigma values were: 10.5, 9.51, and 10.02 for the control conditions (RW, MG, and RT, respectively), and 14.3, 12.4, and 13.9, respectively, for the adapted condition. The horizontal shift between the 2 curves (characterized by the difference in means of the 2 functions) for the 3 different subjects is 22%, 16%, and 12% respectively.

We were interested in quantitatively comparing the magnitudes of the shifts in the psychophysical data with the amount of change in neuronal responses. To do this, we used an opponent model similar in concept to the one developed by the Newsome group (Britten et al. 1992; Shadlen et al. 1996). In this model, each neuron in our sample is paired with a hypothetical "antineuron" with similar properties, preferring the exact opposite direction of motion. Comparison of the rates of each of these neurons will give the decision to whichever of the pair produced the higher firing rate. As coherence rises, the difference between the rates rises and predicted performance improves. Absent adaptation, this model amounts to receiver operating characteristic (ROC) analysis of the difference in firing rates to preferred and null direction test stimuli (Green and Swets 1966). To predict the effects of adaptation, data were taken from the appropriately adapted response functions and compared in the same way. The curves were then fit with probit functions as were the psychophysical functions, and the shift between the adapted and un-adapted curve was calculated. The distribution of these shifts is shown in Fig. 8. While there is some dispersion, the median value from this distribution is 16%, a value nearly identical to the amount of shift seen in our human subjects' performance.
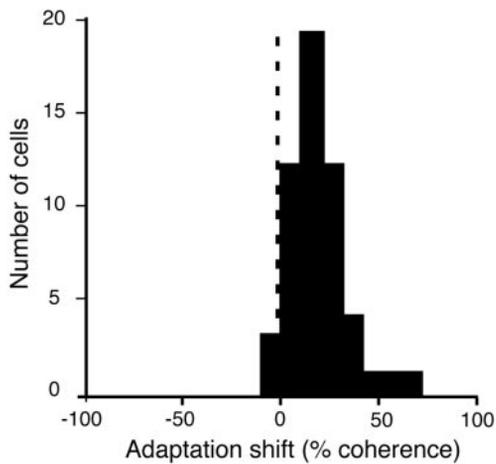
FIG. 8. Shift in neuronal responses. Frequency histogram of the adaptation-induced shift in the neurometric functions of individual MT cells ($n = 53$). For each cell, response curves were transformed into neurometric functions using receiver operating characteristic (ROC) analysis (see Britten et al. 1992), assuming an opponent model. Neurometric functions were fitted with a probit function (see METHODS). The shift was the difference between the mean (horizontal position of the 50%-choice point) of the adapted curve and the control curve.

DISCUSSION

Our experiments produced two main findings. First, MT neurons tuned to a particular direction have attenuated responses following prolonged exposure to stimuli matching their preferences, whereas neurons tuned to the opposite direction are much less affected. Second, under the same stimulus conditions, after motion adaptation in one direction, perceptual decisions regarding motion direction become biased against the preceding adaptation direction, regardless of the test direction. The shifts observed in the psychophysics closely matched the magnitude of the physiological changes.

The most salient result from this work was that adaptation selectively affected MT responses in neurons whose preferences matched the adaptation direction. Elevated responses were only very rarely seen following null direction adaptation. This finding is somewhat different from the only other paper making similar observations in MT (Petersen et al. 1985). In this study, which used much larger, longer-duration adaptation stimuli and smaller, moving-bar test stimuli, some elevation of response was seen following adaptation in the null direction. This finding might be explained because the adapting stimulus extended well into the nonclassical RF surround area, and adaptation of suppressive surround effects might have increased center responses. Alternately, the longer-duration adaptation period might have produced stronger adaptation, revealing effects too weak to be seen in our study. Unfortunately, it will be difficult to test the latter idea, as persuading monkeys to fixate for tens of seconds would be problematic.

Despite the match in magnitude of our physiological and psychophysical results, we found one striking difference as well. In MT, adaptation only systematically affected responses of neurons tuned to the adaptation direction. On the other hand, because the perceptual effects were uniform shifts of the psychometric functions, this indicates that similar effects were obtained for either direction of test stimulus. To best account for this, we needed to impose an opponent step to relate the psychophysics to the perception, which causes asymmetrical physiological effects to become symmetrical perceptual ones. Interestingly, the clear implication of this interpretation is that an opponent step must occur downstream from MT. Most parsimoniously, this step might occur at the level of decision-making or response preparation, because of the forced-choice nature of our task.

While most previous psychophysical studies have found results concordant with those reported here (Blake and Hiris 1993; Lankheet and Verstraten 1995), one study found a somewhat different result. Raymond and Braddick (1996) used test stimuli similar to our own, but only 184 ms in duration. They found results analogous to our physiological results, in that adaptation selectively perturbed the perception of same-direction test stimuli. It seems possible that the duration could influence the opponent mechanisms that our (and other) results point to. Opponency might derive from mutual inhibition among cells tuned to opposed directions (or, equivalently, cells at a later stage of processing, receiving input from such directional cells). Such a circuit might give the opponency slower dynamics than the "feedforward" responses of the directional neurons themselves.

One important mechanistic question concerns whether adaptation effects are subtractive or divisive. Our results provide a mixed message on this question. Single cells are dominated by subtractive effects, yet also demonstrate a modest slope effect that would be a signature of a divisive mechanism (Fig. 5). At the population level, the effects of adaptation appear more divisive (Fig. 6), yet this appearance might be deceptive. Certainly, cells with larger responses show larger effects to the same adapting stimuli. This is almost inevitable, given that "floor effects" would curtail the suppressive effects of adaptation for cells with small baseline responses. However, this need not imply that a divisive mechanism is a work. If each cell receives a stimulus-invariant (subtractive) influence at a given adaptation state, then the population as a whole will also reflect this. Our single cell results, then, we feel to be a good clue as to the cellular or circuit mechanism of adaptation. Our results suggest that the mechanism of adaptation is dominantly subtractive, with only a modest divisive component in addition.

It would be interesting to train monkeys on our psychophysical task and directly compare MT cell responses with monkey behavior. However, there is a fundamental problem with the interpretation of such an experiment. Human subjects can be instructed, as ours were, to give an "honest" answer in an experiment measuring the magnitude of an illusion. Monkeys, on the other hand, cannot be instructed in this way, and will probably change strategy to obtain more rewards depending on the adaptation condition (especially because the difference between adaptation conditions is conspicuous). Therefore any observed bias would probably result from a complex combination of sensory adaptation and cognitive factors, which would detract from the accuracy of the intended comparison. One potential solution to this problem would be to use more objective, strategy-free metrics of directional mechanisms, such as the gain of smooth-pursuit eye movements, to verify the perceptual judgments of the monkeys.

Our results help to clarify the physiological mechanisms underlying the well-studied MAE. Our measurements suggest that under our conditions, there is no above-baseline activity in area MT. In imaging studies of the putative human homologue to area MT, it was originally proposed that fMRI measures of

activity were elevated under conditions where subjects reported perceiving the MAE (Tootell et al. 1995). On the other hand, when differences in attention were eliminated by giving the subjects an attention-demanding foveal task, only reductions in activity were observed (Huk et al. 2001). This more recent finding is entirely consistent with our physiological measurements. Taken together, all these findings strongly support the distribution-shift model of the MAE. Under this model, only decrements in sensitivity (or activity) are seen, and the resulting offset of the overall distribution of activity leads to the positive percept of motion.

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