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Adaptation in Macaque MT Reduces Perceived Speed and Improves Speed Discrimination

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Krekelberg, Bart, Richard J. A. van Wezel, and Thomas D. Albright Adaptation in macaque MT reduces perceived speed and improves speed discrimination. *J Neurophysiol* 95: 255–270, 2006. First published September 28, 2005; doi:10.1152/jn.00750.2005. The visual system adapts to its environment. Some adaptive changes are detrimental—perception is no longer veridical. Others are beneficial—the ability to discriminate two stimuli improves. The latter may reflect the visual system's ability to zoom-in on the currently relevant properties of the environment. We studied the neural basis of adaptive changes in the middle temporal area (MT) of macaque monkey visual cortex. Our data show that brief adaptation to a moving stimulus reduces the magnitude of neural responses and reduces the width of speed tuning curves. Comparable with what has recently been reported in the direction domain, the response reduction was largest when the test speed was different from the adaptation speed. Using an ideal observer analysis, we show that these response changes in MT are consistent with a reduction in perceived speed as well as an improvement in speed discrimination. This supports the view that adaptive response changes in MT are not just a consequence of neural fatigue, but an active process that enhances the discrimination of speed.

INTRODUCTION

Visual perception operates reliably in the face of changes in the visual environment that vary over many orders of magnitude. This is most striking when comparing the average luminance at dusk ($\sim 10^{-2}$ cd/m²) with that at high noon ($\sim 10^5$ cd/m²). Most artificial devices are unable to function over such a range because they lack a fundamental property of the visual brain: adaptation.

It has been hypothesized that the visual system adapts to make efficient use of its limited resources (Barlow and Földiák 1989): if the environment is dark, encoding information on bright objects is useless and sensitivity for dark objects is critical. In other words, to represent information with neurons that have only a limited response range, it pays to zoom in on the properties of the environment and only represent properties that occur often enough to matter but not too often as to be meaningless. Such a change in the neural representation, however, may also have negative consequences: some of the incoming signals may be misinterpreted. We studied this dual view of adaptation at the single cell level.

In particular, we focused on the role of adaptation in the perception of speed. After adaptation, a moving stimulus may appear to move at a different speed (Goldstein 1957; Rapoport 1964; Thompson 1981). We consider this an example of an

undesirable side effect of adaptation: a misinterpretation of subsequent visual stimuli. Speed adaptation, however, also has a beneficial effect: after prolonged exposure to moving stimuli, speed discriminability is increased (Bex et al. 1999; Clifford and Langley 1996; Clifford and Wenderoth 1999; Huk et al. 2001). The latter effect is much more subtle than changes in perceived speed, which may explain why it has not been studied in as much detail. Nevertheless, we believe that the visual system's main goal in motion adaptation is not a reduction in perceived speed but rather improvements in speed discriminability.

We hypothesized that these dual perceptual changes are a consequence of neural changes in cortical visual area middle temporal area (MT). To study this hypothesis, we developed a paradigm that was amenable to testing in awake, behaving monkeys. The main hurdle we faced in doing so was that the long adaptation periods (~ 30 s) used in human research are not feasible with awake monkey subjects. We thus resorted to much shorter adaptation periods (2 s). In the first part of our report we document that these brief adaptation periods elicit small but robust perceptual effects in both humans and monkeys. The qualitative features of brief adaptation were identical to those observed with long adaptation: a reduction in perceived speed, and an improvement in speed discriminability. These findings provided the basis for studying the neural correlates of speed adaptation in macaque MT. We found that MT neurons generally reduced their firing rates even after brief adaptation. Surprisingly, these firing rate reductions were largest for speeds that were different from the adaptation speed. Therefore the changes in the speed tuning curves with adaptation could not be described as a simple scaling factor. Using an ideal observer analysis, we could relate the changes in the shape of the tuning curves to both the reduction in perceived speed and the improvement in speed discriminability.

METHODS

Subjects

Two adult male rhesus monkeys (*Macaca mulatta*; monkeys M and S) were used in the psychophysical and electrophysiological experiments. Experimental protocols were approved by the Salk Institute Animal Care and Use Committee and conform to U.S. Department of Agriculture regulations and to the National Institutes of Health guidelines for humane care and use of laboratory animals.

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A total of five naïve human subjects and one author participated in the psychophysical experiments. The participants gave their informed consent, and all procedures were in accordance with international standards (Declaration of Helsinki) and National Institutes of Health guidelines. All subjects had normal or corrected-to-normal visual acuity.

Surgical preparation

The surgical procedures have been described in detail elsewhere (Dobkins and Albright 1994). In short, a head post and a recording cylinder were affixed to the skull using stainless steel rails, screws, and dental acrylic (monkey M) or CILUX screws and dental acrylic (monkey S). Recording chambers were placed vertically above the anatomical location of area MT as determined from structural MR scans (typically 4 mm posterior to the interaural plane and 17 mm lateral to the midsagittal plane) to allow for a dorso-ventral electrode trajectory. After surgical recovery and attainment of criterion performance on the visual fixation task, a craniotomy was performed to allow for electrode passage into area MT. All surgical procedures were conducted under sterile conditions using isoflurane anesthesia.

Visual stimulation

All visual stimuli were generated with in-house OpenGL software using a high-resolution graphics display controller (Quadro Pro Graphics card, 1,024 × 768 pixels, 8 bits/pixel) operating in a Pentium class computer. In the experiments with monkey subjects, stimuli were displayed on a 21" monitor (Sony GDM-2000TC; 75 Hz, noninterlaced). In the experiments with human subjects, we used a Sony Trinitron E500 monitor. The output of either video monitor was measured with a PR650 photometer (Photo-Research, Chatsworth, CA), and the voltage/luminance relationship was linearized independently for each of the three guns in the monitor. Stimuli were viewed from a distance of 57 cm in a dark room (<0.5 cd/m²).

Monkeys were seated in a standard primate chair (Crist Instruments, Germantown, MD) with the head post rigidly supported by the chair frame. Eye position was sampled at 60 Hz using an infrared video-based system (IScan, Burlington, MA), and the eye position data were monitored and recorded with the CORTEX program (Laboratory of Neuropsychology, NIMH; <http://www.cortex.salk.edu/>), which was also used to implement the behavioral paradigm and to control stimulus presentation.

Stimuli and experimental paradigms

The stimuli used to study speed adaptation were random dot patterns. Each pattern consisted of 100 dots moving coherently in one direction within a 10°-diam circular aperture. The dots were 0.15° in diameter and were 70% more luminous than the gray background (5 cd/m²). The direction of motion of the dots could be adjusted to match the preferred direction of motion of the cells rounded to the nearest multiple of 45°. The speed of the dots was 1, 2, 4, 8, 16, 32, or 64°/s.

Training paradigm

The monkeys were trained to report which of two moving random dot patterns on the screen moved faster. During training, the monkey fixated a central red dot, and two random dot patterns appeared to the left and right of fixation. One moved at least twice as fast as the other. After 0.5 s, the patterns disappeared and were replaced by two red dots. Monkey M was rewarded with a small amount of liquid for making a saccade to the dot at the position of the faster moving pattern. The monkey was required to execute this response within 2,000 ms after onset of the dot target and to maintain fixation on the chosen target for 500 ms. Monkey S was trained to hold two touch bars during stimulus presentation and to release the touch bar below the faster stimulus to indicate his choice. After the monkeys reached criterion (80% correct) performance on this task, we introduced the adaptation phase. At first, we used only adaptation to stationary patterns to introduce the monkey to the longer fixation times required in these adaptation trials. Then, we switched to the complete behavioral paradigm.

Behavioral paradigm to measure changes in perceived speed

Humans and monkeys were tested in almost identical paradigms that consisted of five phases, referred to as the prepare, adaptation, blank, test, and response phases (Fig. 1). We will describe these phases in turn. The differences between the human and monkey paradigms were restricted to the response phase.

In the prepare phase, a small (0.15°) centrally located red spot appeared, and the subjects were required to fixate it. The monkeys' fixation was monitored throughout each trial, and a trial was aborted if the eye position deviated from the fixation point by >1°.

After fixation had been achieved, the adaptation phase started. Two random dot patterns appeared 10° left and right of fixation for 2 s. The two experimental conditions (AdaptNone, AdaptOne) differed only in

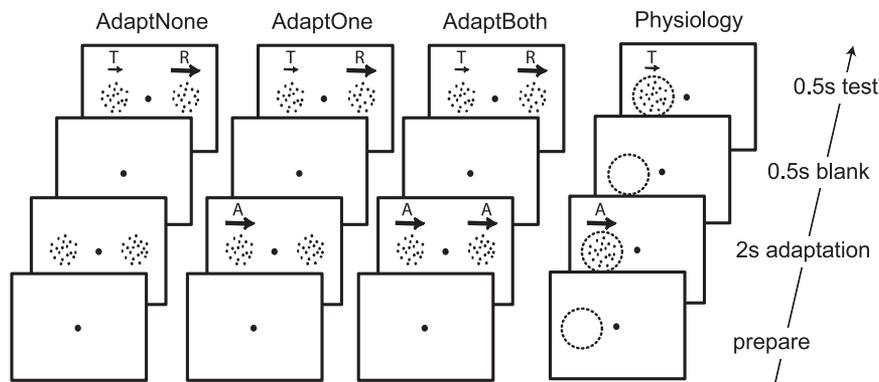


FIG. 1. Experimental design. In the psychophysical paradigms (AdaptNone, AdaptOne, AdaptBoth), a fixation spot appeared, followed by 2 patches of dots on either side of fixation. In the AdaptNone condition, both patches were stationary during adaptation. In the AdaptOne condition, 1 patch contained dots moving at the adaptation speed (A), whereas the right patch was stationary. In the AdaptBoth, both patches moved at the adaptation speed (A). After 2-s adaptation, there was a brief (0.5 s) period in which only the fixation dot was visible, followed by the test phase in which 2 patches with moving dots were visible. In 1 patch, the dots moved at the reference speed R; in the other patch, the dots moved at test speed T. The physiological experiments used the same paradigm but those parts of the stimulus display that were not in the receptive field of the cell were not shown because the behavioral data from the monkeys were not obtained simultaneously. Dashed circle indicates receptive field of the cell under study. Physiology condition shown is an adaptation condition (AdaptOne); in the control condition, stimulus during the adaptation phase was stationary (as in AdaptNone).

terms of the kind of stimuli presented during this adaptation phase. In the control condition (AdaptNone), both random dot patterns were stationary. Because there is no adaptation to motion in this condition, we refer to it as the nonadapted condition. In the AdaptOne condition, one of the random dot patterns was stationary whereas the other random dot pattern moved to the right at a constant adaptation speed (Fig. 1, speed A). Stationary and moving patterns were positioned left and right of the fixation point in a pseudorandom manner and combined in the off-line analysis. In the 0.5-s blank phase that followed the adaptation phase, only the fixation dot was on the screen.

In the test phase, two random dot patterns appeared on the screen, also at 10° left and right of fixation, both moving rightward. For the AdaptOne condition, one pattern, called the reference pattern, was positioned where the stationary pattern was during the adaptation phase. Because of the spatial specificity of motion adaptation (Kohn and Movshon 2003), this reference pattern was therefore nonadapted. In this set of experiments, the speed of the reference pattern was equal to the speed of the adaptation stimulus. In the notation of Fig. 1, $R = A$. To determine the influence of adaptation on perceived speed, we presented a test pattern at the position where the moving pattern was during the adaptation phase. The dots in this test patch moved at 60, 80, 90, 95, 100, 105, 110, 120, or 140% of the reference speed. In the notation of Fig. 1, the speeds T were arranged around R to measure a psychometric curve for speed discrimination. For the monkey, we replaced the 95 and 105% speeds with the easier 30 and 170% speeds.

After the test patterns had been switched off, the response phase started. Human subjects pressed one of two buttons in a two-alternative forced choice to indicate which of the two patterns (left or right) moved faster. Monkey M communicated his decision regarding which stimulus was faster by making a saccade to one of two small red dots that appeared 10° left and right of fixation. Monkey S was trained to release one of two touch bars to indicate his choice. We performed the same experiment at a range of adaptation speeds (Fig. 1A): humans at 4, 8, and 16°/s, monkey M at 4 and 16°/s, and monkey S at 8°/s. All subjects repeated each adaptation speed and test speed combination ≥ 20 times.

In the AdaptNone trials we knew what the monkeys should perceive, and they were rewarded for correct decisions only. In the AdaptOne conditions, we tried to measure the monkey's illusion of speed perception. Not knowing how large the monkey's illusion was, we could not rely on physical speed differences to determine the reward. Based on human pilot data, we estimated that the illusory reduction in perceived speed after adaptation would be at most 20% of the adaptation speed. Therefore we decided to reward all trials with a physical speed difference of $>20\%$ for (physically) correct decisions only. Trials with a speed difference of $<20\%$ were rewarded randomly at a rate of 60%.

Behavioral paradigm to measure changes in speed discrimination

We used a third condition to determine whether speed discrimination improved with a brief 2-s adaptation to motion. This AdaptBoth condition had the same five phases discussed above. In the adaptation phase of the AdaptBoth condition, both patches of random dots moved at the adaptation speed.

In the test phase of this paradigm, two dot patterns (called the reference and the test pattern) that moved at different speeds were shown. For the monkey experiments, the adaptation speed (A) was always 16°/s and the reference speed (R) was 1, 2, 4, 8, 16, 32, or 64°/s. To map out the psychometric curve around this reference speed, the test pattern was assigned a speed (T) that was 5, 10, 20, 40, or 80% slower or faster than the reference speed (R). In all trials of this AdaptBoth condition, both of the patches were adapted. Hence, the reduction in perceived speed should apply equally to both patches. This allowed us to reward Monkey M, who performed this experiment, for veridical speed discrimination in all trials. This consistent

reward was crucial to get a consistent level of performance for small speed differences. For the same reason we did not interleave these conditions with the AdaptOne conditions in which a considerable fraction of trials had to be rewarded randomly. As a control, we did interleave AdaptNone conditions with reference (R) and test (T) speeds identical to those in the AdaptBoth conditions.

For the human subjects, the AdaptBoth trials were interleaved with the AdaptNone and AdaptOne conditions. The choice of adaptation, reference, and test stimuli was therefore the same as in those conditions described above.

Electrophysiological paradigm

We recorded the activity of single units in area MT using tungsten microelectrodes (FHC, 3- to 5-M Ω base impedance), which were driven into cortex using a hydraulic micropositioner (model 650, David Kopf). Neurophysiological signals were filtered, sorted, and stored using the Plexon system (Plexon, Dallas, TX). Off-line spike sorting based on principal components analysis of the waveforms was used to separate up to three cells from a single electrode. We identified area MT physiologically by its characteristically high proportion of cells with directionally selective responses, receptive fields that were small relative to those of neighboring area medial superior temporal area (MST), and its location on the posterior bank of the superior temporal sulcus. The typical recording depth agreed well with the expected anatomical location of MT that was determined from the structural MR scans.

We used automated methods to determine cells' directional selectivity and receptive fields (for details, see Krekelberg and Albright 2005). The receptive field (RF) center and the preferred direction of motion revealed by these methods were used to optimize stimuli for subsequent neuronal response measurements. We determined cells' speed tuning with a random dot pattern positioned at the center of the RF moving in the preferred direction. The dots moved for 500 ms at a constant speed chosen from the set (1, 2, 4, 8, 16, 32, 64°/s). This tuning curve was used to determine the preferred speed. Based on an on-line analysis of the speed tuning curve, we chose one of these speeds as the adaptation speed for the subsequent adaptation paradigm. We aimed to choose a speed that was on the ascending or descending flank of the tuning curve.

To maximize neural data collection, the monkeys did not perform the psychophysical task during recording. Therefore we removed those elements of the display that were relevant for the behavioral task but not for the measurement of the neural responses (Fig. 1). The adaptation stimulus was positioned in the receptive field and it moved in the preferred direction at the chosen adaptation speed (A) for 2 s. After a blank phase of 0.5 s, the test phase consisted of a single test pattern, also positioned at the center of the receptive field, and moving in the preferred direction at one of five speeds. These test speeds (T) were chosen to lie around the adaptation speed. One test speed was identical to the adaptation speed (100%); the other speeds were 20, 60, 140, or 180% of the adaptation speed.

Data analysis

PSYCHOPHYSICAL DATA. We calculated the percentage of trials in which the subjects responded that the test stimulus was faster for each speed of the test stimulus. We used the *psignifit* Matlab toolbox (Wichmann and Hill 2001) to fit these psychometric functions with cumulative Gaussians. This fit provided us with an estimate of the point of subjective equivalence (PSE) and the slope of the psychometric function at that point.

To ensure that the monkey's behavioral was under adequate experimental control, we required that the behavioral performance for the easiest conditions (speed comparisons with $>70\%$ speed difference) was significantly better than 65% correct. For both the perceived

speed experiments and for the discriminability experiment, one session did not match this criterion and was removed from the analysis.

PHYSIOLOGICAL DATA. We analyzed neuronal responses with Matlab (The Mathworks). The measure of neuronal response was the mean spike rate computed within a window of 500 ms (the test stimulus duration) after response onset. Response onset for a given stimulus was defined as the start of the first 50-ms bin in which the firing rate was >3 SD from the baseline firing rate (computed during the initial 250-ms interval during which fixation was maintained but no stimulus was presented in the RF). Response latency was defined as the minimum difference across conditions between stimulus onset and response onset.

Significance of the cell's speed tuning and adaptation was assessed with a Friedman two-factor (speed and adaptation state) ANOVA.

To summarize a cell's speed tuning with three parameters, we used a nonlinear least squares method to fit functions of the following form to the speed tuning data

$$r = \gamma \times (s/\beta)^\alpha \exp\left[-\frac{s}{\beta}\right]$$

In this formula, r is the mean firing rate and s is the speed in degrees per second. Parameter α is the preferred speed, β is the tuning width, and γ scales the peak firing rate.

We defined an adaptation index (AI) to quantify the relative changes in firing rate for every stimulus speed. If the response in an adapted condition is A and the response to the same stimulus without adaptation NA , then $AI = 100\% \times (A - NA)/NA$.

Following Liu and Newsome (2003), we defined a cell as having band-pass speed tuning if the firing rate for speeds both slower and faster than the preferred speed dropped $<90\%$ of the peak firing rate. A cell whose firing rate for all speeds below the preferred speed was $>90\%$ of the peak firing rate was considered low-pass. A cell whose firing rate for all speeds above the preferred speed was $>90\%$ of the peak firing rate was considered high-pass.

Linking neural and behavioral data

We used ROC analysis (Green and Swets 1966) to determine whether an ideal observer using a single threshold firing rate could determine whether a neural response was more likely to have been caused by the nonadapted reference stimulus or 1 of the 10 test stimuli (2 adaptation states \times 5 speeds).

The area under the receiver operating characteristic (ROC) curve was transformed into a perceptual measure reflecting the percentage of trials in which the ideal observer would decide that the test stimulus was faster. This transformation was based on a simplified vector average model of the representation of speed in MT in which neurons cast their vote not for a particular speed, but for whether a stimulus is faster or slower than the preferred speed. For neurons with a preferred speed above the reference speed, the "fraction of trials in which the test stimulus moved faster" was equated with the area under the ROC curve. For neurons with a preferred speed below the reference speed, the fraction of trials in which the test stimulus moved faster was equated with $1 - \text{area under the ROC curve}$. This ordinal code reflects our current ability to relate neural to perceptual data (see DISCUSSION).

In the discriminability analysis, we compared the distribution of nonadapted neural responses to a stimulus with speed S_1 to the nonadapted neural responses to a stimulus with speed S_2 . The resulting ROC curve gave a measure of discriminability of S_1 and S_2 before adaptation. Specifically, we estimated discriminability as the absolute value of the difference between the area under the ROC curve and 0.5. This analysis was repeated using postadaptation distributions of neural responses to S_1 and S_2 .

To quantify the influence of adaptation on discriminability, we subtracted the discriminability of the nonadapted test stimuli from the discriminability of the adapted test stimuli. A value of 0% indicates no

effect of adaptation; positive values mean that an ROC observer would be better at discriminating the speeds of adapted versus nonadapted stimuli.

RESULTS

We have divided the results into three sections. The first section documents that the perceptual changes in a brief adaptation paradigm with human subjects are qualitatively similar to those found using long adaptation periods (e.g., Bex et al. 1999). The main advantage of the brief adaptation paradigm is that we could use it to show that monkey subjects exhibit similar perceptual effects and study the neural correlates of these effects with intracortical recordings. The second section reports the changes in firing rates of macaque MT cells using the same adaptation paradigm. In the third section, we use an ideal observer analysis to relate changes in firing rate to changes in perception.

Perceptual changes

Our psychophysical paradigm is described in detail (see METHODS). Briefly, two patches of random dots were presented for 2 s during the adaptation phase. After a 0.5-s blank interval, two new patches appeared. One patch was called the reference stimulus; the other was the test stimulus. The subject indicated which patch contained the faster moving dots (Fig. 1). There were three conditions, which differed only with respect to the patches that were shown during the adaptation phase. In the control condition (AdaptNone), both patches were stationary during the adaptation phase. In the AdaptOne condition, one patch moved at the adaptation speed, and the other was stationary. This allowed us to measure the change in the perceived speed caused by adaptation. In the AdaptBoth condition, both patches moved at the adaptation speed during the adaptation phase. This third condition allowed us to measure the change in discriminability that follows adaptation, without contamination from a change in perceived speed.

Adaptation reduces perceived speed

Figure 2A shows the performance of one human subject on a speed discrimination task that involved a reference speed of $16^\circ/s$ and many test speeds. The graph plots the probability that the subject reported the test speed to be faster than the reference speed, as a function of the actual test speed. The green curve shows the data from the nonadapted conditions. The curve reaches the 75% test faster response for a test speed near $17^\circ/s$ and the 25% test faster for test speeds near $15^\circ/s$. Hence, in this experiment, the subject's 75%-threshold for speed discrimination was about $1^\circ/s$, which corresponds to 6% of the reference speed. The speed difference at which the psychometric curve crosses 50% test faster is the PSE: a test stimulus moving at this speed was perceived to have the same speed as the reference stimulus. In the AdaptNone condition, the PSE was $15.8^\circ/s$, which is close to the actual reference speed of $16^\circ/s$. The blue curve represents the data from the AdaptOne condition in which the adaptation speed was $16^\circ/s$. Relative to the nonadapted condition (green curve), the blue curve is shifted to the right (PSE = $17.7^\circ/s$). In other words, after adaptation, a test stimulus with a physical speed of $17.7^\circ/s$ was perceived to have the same speed as the nonadapted reference

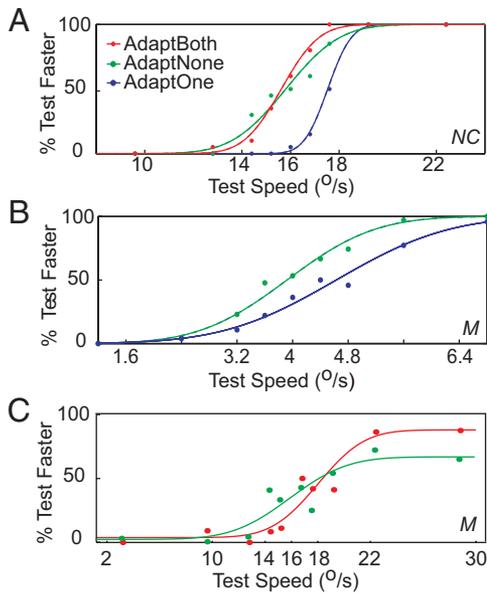


FIG. 2. Perceptual adaptation effects. *A*: psychometric curves from a single human subject with adaptation at $16^\circ/\text{s}$. *B*: psychometric curves from a single monkey subject with adaptation at $4^\circ/\text{s}$. *C*: experiment tailored to measure improvement of speed discrimination with adaptation at $16^\circ/\text{s}$ in a monkey subject. In all 3 panels, green curves show speed discrimination performance without adaptation, blue curves show performance after adapting 1 side with motion, and red curves show performance after adapting both sides. In these experiments, adaptation speed and reference speed were identical (i.e., $16^\circ/\text{s}$ in *A*, $4^\circ/\text{s}$ in *B*, and $16^\circ/\text{s}$ in *C*). These behavioral data show that after only 2 s of adaptation to a moving stimulus, both humans and monkeys perceptually underestimate the speed of a test stimulus, while at the same time, improving their ability to discriminate 2 speeds.

stimulus moving at $16^\circ/\text{s}$. Adaptation in this subject at the adaptation speed of $16^\circ/\text{s}$ thus led to an underestimation of the test speed by about 10%.

Figure 2*B* shows the results from a similar experiment with a monkey subject using a $4^\circ/\text{s}$ reference and adaptation stimulus. In this experiment, the PSE was shifted to the right by $\sim 20\%$ in the AdaptOne condition, which indicates that the monkey—like the human subjects—perceived a reduced speed after adaptation.

To quantify these effects across the population, we determined the PSE from the fitted psychometric curves for each subject and expressed these as a percentage of the adaptation speed. Although the shift in the PSE in humans tended to be somewhat smaller for higher adaptation speeds, this effect was nonsignificant ($P = 0.06$) and even entirely absent for the monkey subjects ($P = 0.7$). We therefore pooled adaptation effects over all adaptation speeds. Figure 3*A* shows a histogram of the adaptation induced shifts in PSE. In all but one experiment the PSE shifted to the right, indicating that subjects typically perceived a reduced speed after adaptation. This effect was statistically significant in both humans and monkeys. (humans mean effect: $16.9 \pm 2.8\%$, $P < 0.01$; monkeys: $5.7 \pm 4.3\%$, $P < 0.05$; signed-rank test).

Adaptation improves discriminability

Figure 2, *A* (human subject) and *C* (monkey subject), documents how adaptation leads to improved discriminability. We first discuss the results obtained in the human subject. The red data points and curve in Fig. 2*A* show the performance on the speed discrimination task in the AdaptBoth condition with a $16^\circ/\text{s}$ reference speed after adaptation to a $16^\circ/\text{s}$ moving pattern. Compared with the AdaptNone condition (green data

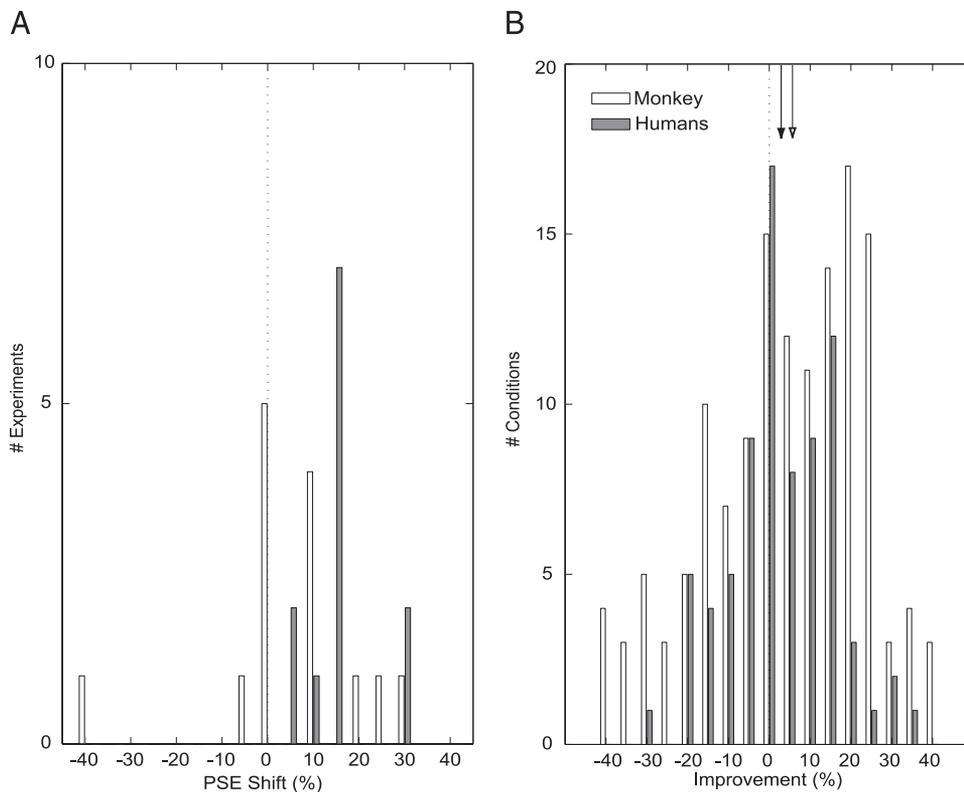


FIG. 3. Perceptual adaptation effects: population overview. *A*: adaptation induced shifts in the point of subjective equivalence (PSE). PSEs are expressed as a fraction of the adaptation speed, and values >0 indicate a decrease in perceived speed after adaptation. Histogram combines experiments with human subjects ($n = 5$) at 2 adaptation speeds and 2 monkey subjects at 2 adaptation speeds. *B*: adaptation induced improvements in speed discrimination. Improvement is calculated per condition (i.e., a particular combination of adaptation speed and test speed) and expressed as the difference between percentage correct before and after adaptation. Solid and open arrows point to the population average of the human and monkey data, respectively. These behavioral data clearly show that both humans and monkeys underestimate true speed after only 2-s adaptation but, at the same time, improve their speed discrimination performance.

points), the psychometric curve was clearly steeper. For test speeds either faster or slower than the reference speed, the subject responded with the correct answer on a larger fraction of the trials. To quantify this effect, we simply determined the difference between the percentage correct answers in the adapted and unadapted conditions for each test speed. For this subject, the average of this difference over all test speeds was a particularly large improvement of 16%.

Figure 2C shows the results of one behavioral session for monkey M. Monkey M's overall performance was clearly not as good as that of the human subjects. To perform at 75% correct, this monkey required a speed difference of ~20%. Monkey S had very similar thresholds (data not shown). As is evident from the figure, after adaptation (to 16°/s), monkey M's psychometric curve (red) was steeper than without adaptation (green). This means that—after adaptation—smaller speed differences led to higher levels of performance. Moreover, the higher asymptote of the red curve shows that, after adaptation, the monkey reached levels of performance for test speeds >16°/s that were never reached in the unadapted conditions. Both the steeper slope and the higher asymptote indicate an improvement in speed discrimination. We quantified this improvement again by simply comparing the percentage correct in the adapted and nonadapted conditions. In this experiment, adaptation improved Monkey M's performance on the speed discrimination task by 17%.

The improvement data are summarized across the population in Fig. 3B. Averaged across all conditions, the human subjects showed a median improvement of 3% ($P < 0.01$; signed-rank test), whereas monkey M showed an improvement of 6% ($P < 0.01$; signed-rank test).

Making use of the large number of trials obtainable from the monkey subject, we also studied whether adaptation at one speed improves discrimination performance at different speeds. Specifically, for a single adaptation speed (16°/s), the monkey was tested on speed discriminations involving reference speeds that were more than twice as fast or slow (see METHODS). No statistically significant improvement was found for any of those speeds (data not shown). In other words, adaptation at 16°/s only improved discrimination performance significantly ($P < 0.05$, 2-way ANOVA) for comparisons that involved the 16°/s reference speed and speeds in a range close to it. In the physiological experiments, we only studied the range of speeds close to the adaptation speed (see METHODS).

To summarize, our behavioral experiments show that 2 s of adaptation to a moving stimulus leads to a perceptual underestimation of absolute speed but an improved ability to discriminate the adapting speed from other speeds. This phenomenon was observed in both humans and monkeys. Having thus documented that the perceptual phenomenon of interest occurs in both humans and monkeys, we turned to the neural signals that we hypothesized to be responsible for these perceptual changes.

Neural changes

To study the neural basis of changes in speed perception with adaptation, we recorded from 83 cells in area MT of two monkeys (S: 41 cells; M: 42 cells) at eccentricities ranging from 3 to 15°, with a median eccentricity of 8°. We analyzed and classified the basic speed tuning properties of these cells

using standard procedures explained in METHODS. As expected, and in agreement with earlier findings (Rodman and Albright 1987), a majority of the cells (69/83; 83%) was significantly speed tuned. We restricted our analyses to these cells. Most cells (77%) were band-pass speed-tuned, 4% were low-pass tuned, and 19% high-pass tuned. These relative proportions of tuning types agree well with the proportions found in another recent study of speed tuning in area MT (Liu and Newsome 2003). The distribution of preferred speeds was broad; the quartile range extended from 7.5 to 30°/s, with a median of 19°/s. This too is in qualitative agreement with previous findings (Churchland and Lisberger 2001; DeAngelis and Uka 2003; Rodman and Albright 1987; Van Essen 1985) from area MT.

Adaptation reduces firing rate

Adaptation typically reduced the firing rate of MT neurons. Averaged over all cells and all test speeds, a reduction in firing was observed in 70% of cases. To assess the statistical significance of rate changes with adaptation, we performed a two-way ANOVA with speed and adaptation state (adapted/non-adapted) as the factors (see METHODS). This analysis showed that 27 cells (39%) showed a statistically significant change in response rate after adaptation. For cells exhibiting a statistically significant adaptation effect, a rate reduction was observed in 87% of cases; hence adaptation almost never led to an increase in firing rate.

To control for the possibility that the animals' fixational eye movements contributed to the adaptation effects, we analyzed eye position and microsaccades for each recording. The average eye position did not depend significantly on stimulus condition in any recording. For the speed and direction of small eye movements (within the fixation window), we found a significant effect for only 3 of 34 recordings. There was no indication that these recordings with a significant change in microsaccade distribution also were the recordings with the significant adaptation effect. In fact, of the cells with a significant adaptation effect, none had a significant microsaccade effect. Overall, there was no indication that eye movements were in any way correlated with the presence or absence of adaptation effects.

The magnitude of the adaptation effect often varied with the test speed. Four typical examples, covering the range of effects we observed, are shown in Fig. 4. These graphs plot the average firing rate in a 500-ms response window as a function of the physical speed of the random dot stimulus (moving in the preferred direction). Solid lines connect data points that were recorded without previous adaptation to motion; dotted lines connect data points recorded after 2 s of adaptation to motion (in the preferred direction). The arrows indicate the adaptation speed. Figure 4, A and B, shows data from cells that preferred higher speeds; after adaptation, the firing rate showed a general decrease. Figure 4, C and D, shows data from cells that preferred lower speeds; firing rates were reduced after adaptation.

To quantify the effect of adaptation on overall firing rate, we defined an AI as the change in firing rate caused by adaptation relative to the response before adaptation (see METHODS). A negative AI indicates that adaptation reduced the firing rate; 0% means no effect of adaptation. This index was calculated

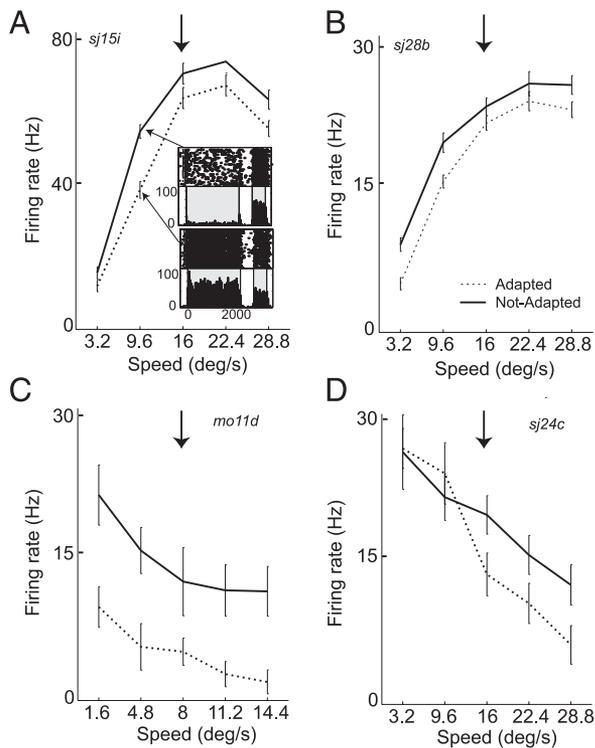


FIG. 4. Single cell adaptation effects. *A–D*: solid lines show nonadapted responses; dotted lines show response after 2 s of adaptation. *Insets* in *A* show raster plots and peristimulus time histograms (PSTHs; spikes/s vs. time in ms) corresponding to the condition in which the test stimulus moved at 9.6°/s. Gray backgrounds in the PSTHs represent the epochs of adaptation and test, respectively. Error bars indicate SE. Vertical arrows indicate adaptation speed. Cells in *A*, *B*, and *D* were adapted at 16°/s; cell in *C* was adapted at 8°/s. These representative examples show neural responses in middle temporal area (MT) are typically reduced even after only 2 s of adaptation to a moving stimulus.

separately for each test speed. The grand average of this index over all cells was -8% (or -18% for the cells that showed a statistically significant adaptation effect), but this grand average over all test speeds hides some of the interesting details.

Adaptation changes speed tuning

In this section, we aim to find a parsimonious description of the relation between the adaptation effect and the other properties of the neurons. The analyses reported in this section were applied to all 69 cells, but we found qualitatively similar results in the subset of significantly adapting cells. We first tested two simple intuitive hypotheses. The first hypothesis was that the adaptation is a fixed, test-speed independent, reduction in firing. This kind of subtractive relationship would, for instance, be expected if the response during the adaptation phase caused an increase in firing threshold. To test this hypothesis, we determined the average (over all test speeds) adaptation-induced reduction in firing per cell, and subtracted this from the unadapted response for each test speed. We compared this predicted adapted response to the actual adapted response. If the subtractive model was correct, one would expect the residuals (the difference between predicted and actual response) to be “noise.” That is, they should be normally distributed around zero. This was not the case (Lillie test; $P < 0.01$). Notably, the adaptation was systematically underestimated at high firing rates. This suggests that a divisive, not a subtractive mechanism is at work.

This leads us to the second hypothesis, which we refer to as neural fatigue. In this model, the adaptation effect increases with the firing rate evoked during the test period. We tested this divisive model in a similar way. First, we determined the best divisive factor per cell by averaging the adaptation ratio over all speeds. Then we predicted the adapted response by multiplying the unadapted responses with the same factor. The residuals of the divisive model were smaller than those of the subtractive model, hence the divisive model was better. However, the residuals were not normally distributed (Lillie test; $P < 0.01$). This suggests that this model also fails to capture a systematic component in the data. In other words, the dependence of adaptation on the test speed is more complex than a simple subtraction or division by a constant factor.

To study the dependence of adaptation on test speed more thoroughly, we determined the adaptation index for each test speed, sorted the indices by the unadapted response at that test speed and binned and averaged the adaptation indices over all cells. These average adaptation indices are represented by the solid curve in Fig. 5*A*. The rightmost data point contains the average adaptation index for conditions in which the unadapted neural response for a given cell was 85–100% of the maximum response for that cell. Hence, it represents the typical magnitude of adaptation found near the peak of a cell’s tuning curve. The leftmost data point represents the average adaptation found for test speeds that were far from a cell’s optimal speed. Figure 5*A* strongly argues against adaptation as neural fatigue. There was a significant (Kruskal-Wallis ANOVA; $P < 0.01$) effect of the normalized firing rate on the adaptation index, but it was opposite to what would be expected if fatigue were the underlying mechanism. The adaptation was largest (the index most negative) at nonoptimal speeds, reached a minimum for stimuli with intermediate efficacy then became larger again at the peak of the tuning curve.

One interpretation of the adaptation effects, shown by the solid line in Fig. 5*A*, is that adaptation was smallest on the flanks of the tuning curve, near 70% of the peak firing rate. There is, however, a confounding factor in this analysis. The average adaptation effect does not take into account that not all cells were adapted at the same speed. To show this, the histogram in Fig. 5*A* represents the distribution of responses to the adaptation stimulus. We deliberately chose the adaptation speed to lie on the flank of a cell’s tuning curve, and the histogram confirms this: most adaptation speeds evoked a firing rate between 50 and 85% of the peak firing rate. This implies, however, that the choice of adaptation speed was confounded with the preferred speed of a cell. An alternative interpretation of the speed dependence of adaptation is that adaptation is weakest near the adaptation speed and increases for test speeds different from the adaptation speed. This is suggested by the fact that the smallest amount of adaptation (peak of the solid line) occurs for the firing rates typically evoked by the adaptation stimulus (peak in the histogram).

In Fig. 5*B*, we tested this interpretation of the test speed dependence of adaptation more directly. The scatter plot shows a cell-by-cell comparison of the AI for the condition in which the test speed equaled the adaptation speed versus the AI observed at the other four test speeds. Red dots represent cells that have statistically significant adaptation effects. The first observation is that the data points are not homogeneously

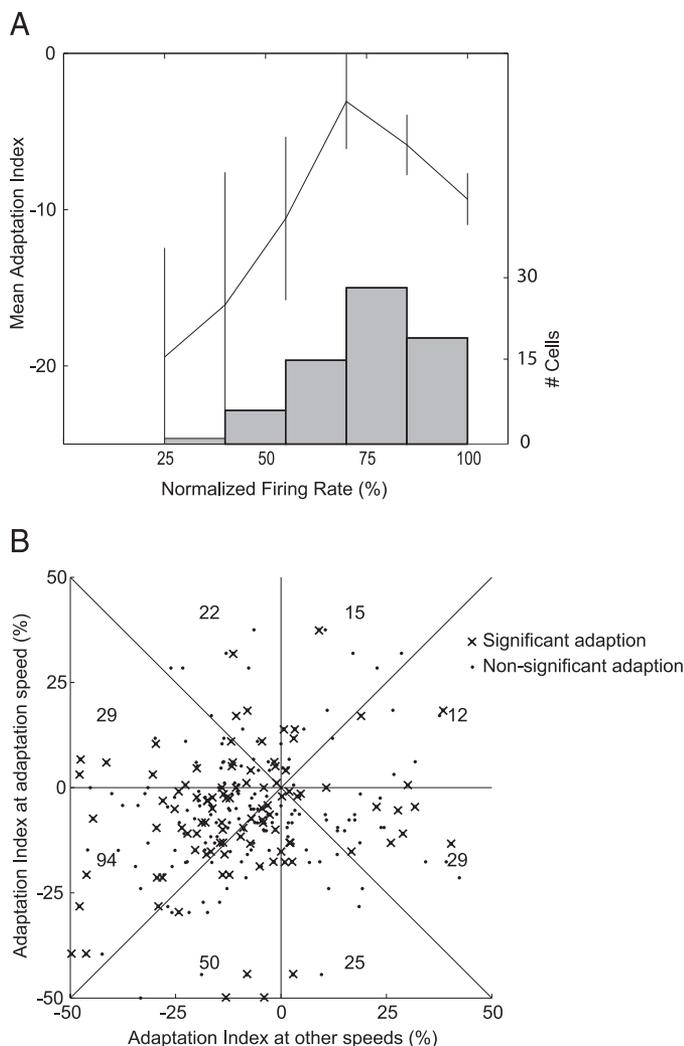


FIG. 5. Speed dependent adaptation effects. *A*: solid curve shows relationship between adaptation index for a given test stimulus and response that the same test stimulus evokes before adaptation. Normalized firing rate (horizontal axis) is defined as the percentage of peak firing rate that a test stimulus evokes. Adaptation measured with test stimuli that evoke a firing rate within 15% of the peak firing rate are averaged in the rightmost data point. Adaptation for stimuli that are very ineffective for a given cell (firing rate between 0 and 15% of the peak) are averaged in the leftmost data point. Solid curve averages over all recordings, regardless of speed of adaptation stimulus that was used. Histogram gives some insight into choice of adaptation speeds. It represents the number of cells (right axis) adapted with stimuli that evoked the given normalized firing rate. Peak of the histogram lies near 70%, which means that most adaptation stimuli evoked a firing rate corresponding to 70% of peak firing rate. In other words, most adaptation stimuli were on the flank of the tuning curve. *B*: scatter plot comparing adaptation measured at adapted speed with those at speeds that were 20, 60, 140, and 180% of adaptation speed. Each dot represents 1 comparison for a single cell. Red dots indicate cells for which adaptation effect was statistically significant. Numbers in each octant indicate number of data points that fall within that octant. Together, *A* and *B* show that the effect of adaptation is not largest at the peak of the tuning curve (prediction of a neural fatigue view of adaptation). Effect of adaptation is minimal for speeds equal to adaptation speed, and increases for test speeds were different from adaptation speed.

distributed (χ^2 test, $P < 0.001$): most data points are found in the bottom left quadrant. This confirms that, for most conditions, firing rates decreased with adaptation. Within the bottom left quadrant, 50 data points are in the lower octant, whereas nearly twice as many (94) are in the upper octant. This shows that most cells exhibited less adaptation when the test stimulus

moved at the adaptation speed than when the test stimulus moved at any of the other four test speeds. This was confirmed statistically with a signed-rank test ($P < 0.01$).

Figure 5*B* suggests that the adaptation effect increases when the test speed is different from the adaptation speed. However, the alternative model suggested by Fig. 5*A*, that adaptation increases with distance from the flank of the tuning curve, has not yet been disproved. To address this issue, we first defined the flank as a firing rate of $75 \pm 10\%$ of the peak firing rate. We selected the cells in our population where the adaptation speed and the flank of the tuning curve did not coincide. Only these recordings provide information to distinguish the two models. For these cells ($n = 32$), we repeated the analysis in Fig. 5*B* and confirmed a statistically significant reduction of adaptation for test speeds near the adaptation speed ($P < 0.01$). We performed the same analysis to compare the adaptation effect on the flank with that found for the other four test speeds. There was no statistically significant effect ($P = 0.31$). This analysis shows that the adaptation depended on the difference between test and adaptation speed, not on whether the test speed was close to the flank of the tuning curve.

This trend can be observed directly in the single cell examples of Fig. 4. For instance, the cell in Fig. 4*C* adapted least at the adaptation speed. There were, however, clear exceptions to this rule. For instance, adaptation in the cell shown in Fig. 4*D* clearly increased with distance from the preferred speed rather than the adaptation speed.

To determine how general the test speed dependence of adaptation was, we performed the analysis shown in Fig. 5 on various subsets of the data. First, we studied whether the response window used for the analysis was relevant by using only the transient (1st 100 ms) or only the sustained (last 400 ms) part of the response to the test stimulus. The adaptation effects in the transient and sustained windows were not significantly different ($P = 0.4$, signed-rank test) and both response windows showed effects that were qualitatively similar to those shown in Fig. 5. Second, we analyzed the adaptation separately for the subset of cells with low preferred speeds ($< 16^\circ/\text{s}$) and high preferred speeds ($\geq 16^\circ/\text{s}$). The test speed dependence of adaptation for both subsets was qualitatively similar to that shown in Fig. 5. To summarize, these analyses show that the finding that adaptation is largest for test speeds other than the adaptation speed is a general one; it does not depend on the window of analysis, nor is it restricted to particular subclasses of cells.

Parametric changes in speed tuning

The analysis in the previous section allowed us to compare the adaptation effects evoked at various test speeds. Additionally, we performed a parametric analysis to quantify global changes in tuning at the population level. We fitted tuning curves (see METHODS) to the mean responses, separately for adapted and nonadapted conditions. Because the test speeds were chosen per cell to lie on the flank of the tuning curve, not every recording resulted in a good coverage of the tuning curve. To avoid over interpreting poorly fitted curves, we used only cells for which the fitted curve explained $> 75\%$ of the variance ($n = 49$). For these cells, the fitted tuning curves provided an estimate of the peak firing rate, the preferred speed, and the width of the tuning curve. Figure 6 compares

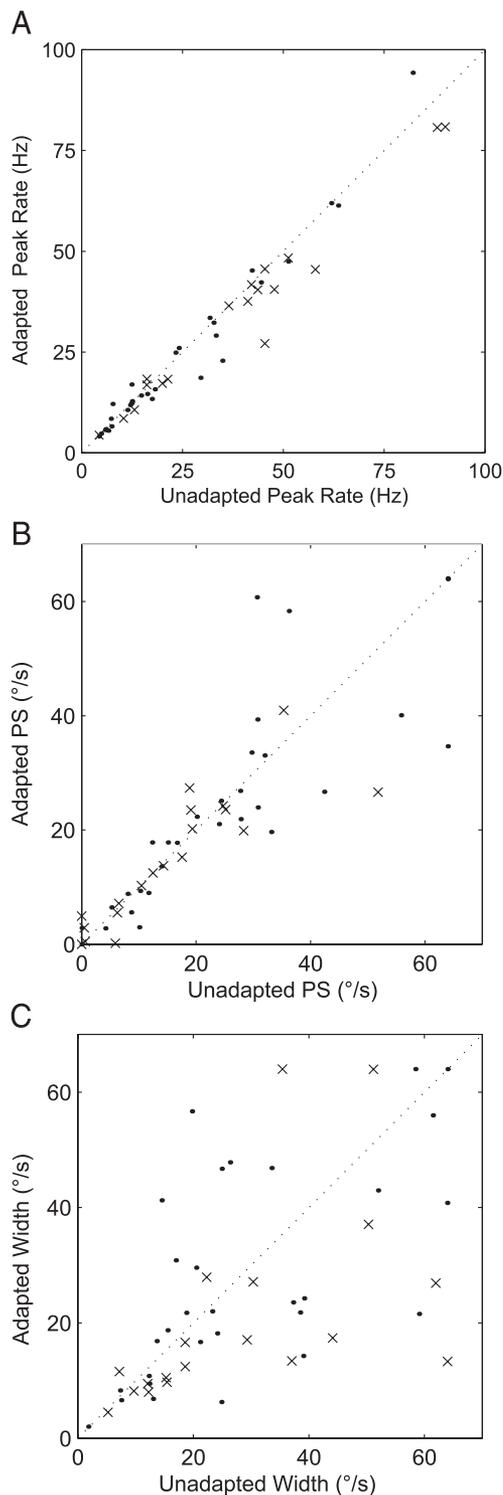


FIG. 6. Population changes in speed tuning. *A*: comparison of (fitted) peak firing rate before (*x*-axis) and after (*y*-axis) adaptation. *B*: comparison of adapted and nonadapted preferred speed. *C*: comparison of adapted and nonadapted tuning width. Each dot represents a single cell, and we selected only those 49 cells for which the fit of the tuning curve explained $\geq 75\%$ of the variance. Crosses show subset of 19 cells for which the adaptation effect was individually statistically significant.

these three quantities in the adapted and nonadapted state. In Fig. 6*A*, we plotted the adapted peak firing rate as a function of the nonadapted peak firing rate. Most cells lie below the diagonal line; hence adaptation reduced peak firing. This effect

was small, but significant at the population level ($n = 49$; 0.7 Hz; $P < 0.01$) and for the subset of significantly adapting cells ($n = 19$; 2.9 Hz; $P < 0.01$). Figure 6*B* shows that adaptation did not significantly effect the preferred speed ($P > 0.7$). Finally, Fig. 6*C* shows that the width of the tuning curve was reduced after adaptation. This was a nonsignificant trend at the whole population level ($n = 49$; 2.7°/s; $P = 0.09$), but significant for the cells that showed a statistically significant adaptation effect ($n = 19$; 4.3°/s; $P < 0.05$). These results show that adaptation led to narrower tuning curves, with a lower peak, but the same preferred speed.

Linking neural and perceptual changes

To compare the speeds of two stimuli—A and B—a decision mechanism must compare a neural response to stimulus A with a neural response to stimulus B. One technical difficulty is that on any given trial, we, the experimenters, only obtained information about the response to one stimulus (say A, the stimulus that was in the receptive field of the cell under study in this trial). To study speed discrimination with such data, we used information from trials in which stimulus B was in the receptive field. Of course, the brain of an observer doing a discrimination task cannot solve the problem this way. One conceptual way to link this analysis to a decision process that could be implemented in the brain is to use a so-called antineuron. In this conceptualization one assumes that there is a neuron that is identical to the neuron under study in all respects, except for its tuning in the stimulus dimension about which a decision is to be made. Britten et al. (1992) were the first to use this technique to relate the firing of direction tuned neurons to perceptual decisions about direction. In that case, direction was the relevant stimulus dimension; hence they introduced antineurons with a direction tuning opposite to the direction tuning of the neuron under study. Because the decision we tried to model was one of position (*where* is the faster stimulus?), our antineuron had the same speed tuning but a different spatial receptive field. Hence for the decision A versus B, we used the responses of our neuron from trials in which stimulus A was in the receptive field and for the antineuron we used the trials in which stimulus B was in the receptive field of the neuron. With this foundation, we modeled speed discrimination as a comparison of the neural responses to stimulus A versus those to stimulus B. If these responses were very different, it should be possible for a decision mechanism that compares inputs from the neuron and its antineuron to infer that the stimuli were different.

We first wanted to determine whether it is reasonable to suppose that the monkey used a population of MT cells to perform a speed discrimination task in which a test and a reference speed are compared. We compared the monkey's behavioral performance with the performance of an ideal observer that based its decisions on the responses of individual MT neurons. To be specific, we determined the expected performance of an ideal observer by calculating an ROC that compared the distribution of responses to the reference stimulus with the distribution of responses to a test stimulus. The area under the ROC curve estimates the percentage correct performance of an observer that uses a single (but arbitrary) threshold firing rate to determine whether a particular response is more likely to have been caused by stimulus A than stimulus

B (Green and Swets 1966). The ROC approach is reasonably general, biologically plausible, and has been used in other contexts to link neural firing with perceptual decision processes (Britten et al. 1992, 1996; Croner and Albright 1999; Thiele et al. 2000). The percentage correct (discriminability) of the ideal observer is of course bounded by 50 (chance level) and 100% (perfect performance). Thirty-eight cells were tested with the same reference speed of 16°/s. In Fig. 7, we compared the performance of the ideal observer based on those 38 cells with the behavioral performance of a monkey subject presented with the same set of reference and test stimuli.

The horizontal axis identifies the test speed that was compared with the reference speed of 16°/s. The range of the monkey's performance (spanning the 25th to the 75th percentile over 15 days) is shown in red; on average, the monkey got ~80% of the trials correct when the difference in speed was $\geq 40\%$. However, there was a considerable spread in the performance over days. In comparing these behavioral data to the neural data, it is important to recognize that not every cell is suitable for every speed comparison. In particular, if the two speeds to be compared are near the (flat) peak of a cell's tuning curve, the firing rate difference will be small, and hence, the ideal observer will not obtain much information from this cell. Compare for instance the cell in Fig. 4B with that in Fig. 4D. The cell in Fig. 4B peaked near 22°/s and there was only a small difference in firing evoked by a 22.4 and 16°/s stimulus. Hence, this cell provided little information for this particular speed discrimination. The speed tuning curve of the cell in Fig. 4D, on the other hand, peaked at 3.2°/s, and it had its steepest slope near 16°/s. This cell provided most information for comparisons of 16°/s with higher speeds.

To show this, we calculated each cell's performance for all speeds and divided the cells into two subpopulations on the basis of their discrimination performance for speeds lower and higher than the reference speed. If a cell was best at discriminating higher speeds from the 16°/s reference speed, it was assigned to the "above" population ($n = 11$). If a cell per-

formed best at discriminating lower speeds from the 16°/s reference speed, it was assigned to the "below" population ($n = 27$). Note that this subdivision was based on the neurons' performance on a perceptual task (the ROC analysis) and not whether these cells are tuned for high or low speeds. This subdivision is clearly arbitrary and only serves to show the point that subdividing the population can be beneficial. On the basis of our data, we cannot make any claims whether the brain actually follows the procedure we used to define the subpopulations.

Figure 7 shows the performance of the below population in blue. For the discrimination that involved the lowest test speed (3.2°/s) and the 16°/s reference, the ROC observer's performance spanned a range that was similar to that of the monkey. Typically, however, these cells' tuning curves reached their peaks in the range of 16–32°/s. The resulting shallow slope of the speed tuning curve in the range of high speeds explains why an ROC observer that relies on these below cells performs relatively poorly on the discrimination of 16°/s with 22.4 or 28.8°/s. The performance of an ROC observer using cells from the above population is shown in green. These cells peaked at lower speeds and exhibited a large difference in firing rate between 16 and 28.8°/s. This difference in firing rate enabled the above population to provide information where the below population could not. Even for these two small populations, the differences in performance was statistically significant ($P < 0.01$) for all but the 9.6°/s test speed (2-way ANOVA; interaction; $P < 0.01$, followed by Tukey-Kramer multiple comparison tests).

This analysis shows that for part of the range of behavioral performances of the monkey, there were single MT cells that provided enough information. On some days and in particular for the comparisons involving the smallest speed differences, however, the monkey outperformed most of its cells. This suggests that the monkey's decision must be based on pooled information provided by a number of cells and that this number may be larger for the more difficult discriminations. Figure 7

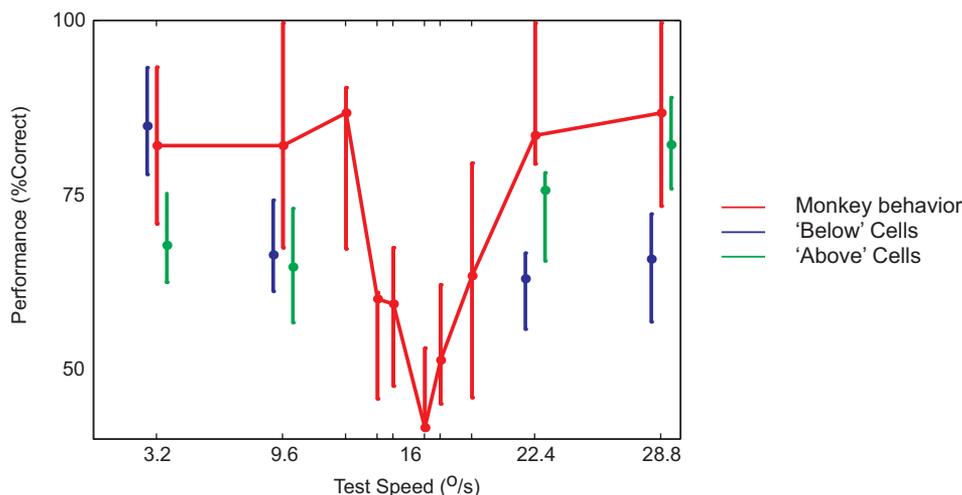


FIG. 7. A comparison of neurometric and psychometric speed discrimination. Red data points represent average performance of the monkey on the speed discrimination task involving a 16°/s reference stimulus and a test stimulus, with speed shown on the x-axis. Blue data points show performance expected of an ideal observer that relies on a single prototypical MT cell chosen from the "below" group of cells. These cells, by definition, perform best for speed discriminations with stimuli $< 16^\circ/\text{s}$. Green data points show performance of an ideal observer relying on a prototypical single MT cell chosen from the "above" group of cells. These cells perform best at discriminating higher speeds from 16°/s. Error bars show range spanning from 25th to 75th percentile. Animal's speed discrimination performance is often somewhat better than that of the ideal observer relying on these typical single MT neurons. This suggests that the animal may pool information over a (relatively small) number of MT cells.

also shows that different pools of cells provide pertinent information for different speed discriminations. Hence selecting specific subpopulations for pooling would be a worthwhile strategy. With current knowledge of MT, however, it is not clear how the speed information is pooled nor is it clear whether and how the decision process selects suitable subpopulations for pooling.

In what follows, we will side-step these pooling issues and simply determine the average performance based on single cells. This average provides insight into the performance that could be expected from the average cell. If a population of such cells were independent, the performance would simply scale with the number of cells. Correlations between the cells, however, would limit this increase in performance (Shadlen et al. 1996). It seems likely that the true decision process uses more sophisticated methods than simple summation. Exploration of the simplest pooling and selection mechanisms, however, provides insight into the representation of speed in MT, as well as the influence of adaptation on this representation.

Adaptation reduces perceived speed

In the psychophysical tasks that studied changes in the percept of speed with adaptation (AdaptNone and AdaptOne), subjects compared the nonadapted reference stimulus to a range of nonadapted and adapted test stimuli. At the level of an MT cell, this means that the relevant ingredients for the decision process are the response to the nonadapted reference stimulus and the response to one of the test stimuli.

We used a simplified version of the vector average labeled line model to relate neural activity to speed perception (Churchland and Lisberger 2001; Priebe and Lisberger 2004). In the vector average model, each cell votes for its preferred speed with a weight proportional to its firing rate, and the speed percept is decoded as the weighted average of these votes. The precise nature of the weighting and distribution of the labels (preferred speeds) have a strong influence on the quantitative outcome of this model. In fact, in previous work (Churchland and Lisberger 2001; Priebe and Lisberger 2004) this model has not been used to decode veridical speed information. The model can, however, successfully account for ordinal effects of

stimulus changes on speed perception. For example, entering MT firing rates recorded for high spatial frequency gratings into the model leads to a lower decoded speed than entering the firing rates recorded for low spatial frequency gratings. This ordinal relationship (high spatial frequency looks slower) also holds perceptually (Priebe and Lisberger 2004). Typically, psychophysical experiments provide direct access only to ordinal relationships. In our behavioral experiments, for instance, subjects were asked to judge which of two stimuli was faster. Hence, to link the neural data to the behavioral data we only had to specify how neural firing is related to the concept of "faster."

Our simplification of the vector average model therefore used only ordinal labels. If the preferred speed of the cell was higher than the reference speed, the cell voted for faster. We refer to these cells as high-ps cells. Conversely, if the preferred speed of the cell was lower than the reference speed, it voted for slower (low-ps cells). This direct mapping of the neural activity to the two alternative forced choice (2AFC) task also allowed us to use the ROC analysis to estimate the weight of the vote: the larger the area under the ROC curve, the stronger the vote. In other words, the area under the ROC curve mapped directly onto an estimate of the fraction of trials in which an ideal observer would decide that the test stimulus was faster (or slower).

To show this decoding process, first consider the unadapted tuning curve of the high-ps cell in Fig. 4B. The ROC analysis showed that, in 80% of trials, a stimulus moving at 28.8°/s evoked a larger response than a stimulus moving at 16°/s. The preferred speed of the cell was higher than the reference speed; hence we interpreted the increase in firing rate as a vote for an increase in speed. Using this code, we could therefore translate the statement: in 80% of trials, the stimulus moving at 28.8°/s evoked a higher firing rate than the stimulus moving at 16°/s into the statement: in 80% of trials the ideal observer concluded that the 28.8°/s test stimulus *moved faster* than the 16°/s reference stimulus.

We applied the same analysis and the same code to all test speeds to generate the nonadapted neurometric curve (solid line) in Fig. 8A. The same ROC analysis and the same code were then used for comparisons of the adapted responses to the test stimuli and the nonadapted responses to the reference

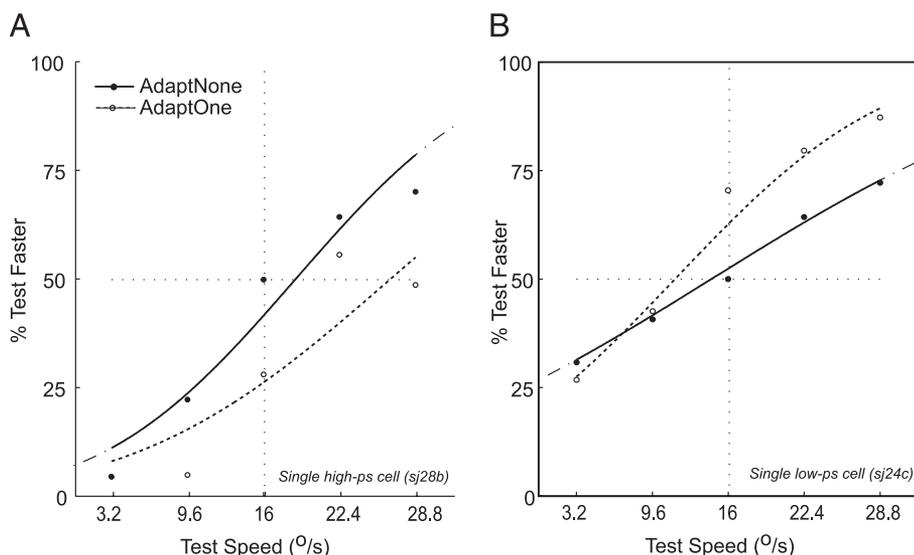


FIG. 8. Neurometric speed curves. *A*: performance of an ideal observer relying on the cell whose tuning curve is shown in Fig. 4B. *B*: performance of an ideal observer relying on the cell shown in Fig. 4D. Solid curves and symbols show performance before adaptation (comparable with the AdaptNone condition in Fig. 2). Dashed curves and open symbols show performances after 1 of the patches has been adapted (AdaptOne). Curves fitted to data points are cumulative Gaussians; their purpose is to guide the eye; they were not used in analysis. Relying on these cells, the ideal observer would report a decrease in perceived speed (*A*) or an increase in perceived speed (*B*) after adaptation.

stimulus. This resulted in the adapted neurometric curve (dashed line). For this cell, the comparison of a 28.8°/s test stimulus after adaptation with the 16°/s reference stimulus resulted in a “test faster” response in only ~50% of trials. In other words, the perceived speed of the test stimulus was reduced after adaptation. This reduction in perceived speed was found for all test speeds presented to this cell, as witnessed by the rightward shift in the neurometric curve. This rightward shift matched the rightward shifts seen in the psychometric curves of the AdaptOne condition in Fig. 2, A and B, and it can be compared with the change in the tuning curve of this cell shown in Fig. 4B.

A significant part (35%) of the population, however, had preferred speeds that were lower than the reference speed. For these low-ps cells (e.g., Fig. 4D), we interpreted an increase in firing as a decrease in speed. Hence, if the ROC analysis showed that in 75% of trials the ROC observer would conclude that the firing rate to the test stimulus was higher than that to the reference stimulus, that would be translated to in 25% of trials, the ROC observer would conclude that the test speed was faster.

Figure 8B shows the neurometric curves based on this linking assumption for the cell in Fig. 4D. Note how the psychometric curves are inverted compared with the firing rate tuning curves of Fig. 4D. For this cell, adaptation shifts the neurometric curve to the left, suggesting that, for the ideal observer relying on this cell, adaptation should lead to an increase in perceived speed.

As the neurometric effects clearly vary across cell types, it is important to quantify the behavior of the population. To average over cells, we expressed all test speeds as a percentage of the adaptation/reference speed. We determined the neurometric curves per cell (as shown for 2 cells in Fig. 8) and averaged those over all cells. Figure 9A shows the average neurometric curve for the high-ps neurons in our sample ($n = 52$). The average neurometric curve undergoes a rightward

shift with adaptation that corresponds to ~29% of the adaptation speed. A two-way ANOVA showed that the effect of adaptation was significant ($P < 0.01$). An ROC observer relying on this subpopulation should report test stimuli to be slower after adaptation. Figure 9B shows the same analysis applied to the low-ps cells in our sample ($n = 17$). Here adaptation also shifts the neurometric curve, but now ~22% to the left, which suggests that the ROC observer relying on this subpopulation should report test stimuli to be faster after adaptation. This effect was also statistically significant ($P < 0.01$).

These analyses show how the representation of speed in area MT changes after adaptation. The effect that these neuronal changes will have on behavior depends on two factors. The first factor is the speed at which the adaptation took place, because that determines which of the cells in the population will respond and which cells will adapt. The second factor on which the behavioral effect will depend is the pooling mechanism that combines speed information from multiple cells. To deal with the first issue, we related the physiological changes in the population to the behavioral experiments by analyzing only those 38 cells where the adaptation speed was the same as in one of the behavioral experiments (16°/s). The second issue is more difficult to address, because current understanding of pooling and decision processes is only rudimentary. In Fig. 9C, we assumed the simplest pooling mechanism; a simple average over all cells. Because the high-ps cells showed slightly larger effects (cf. Fig. 9, A with B) and there were more of them, the average population effect was a 14% rightward shift. Here too, the effect of adaptation was statistically significant according to the two-way Friedman ANOVA ($P < 0.05$). In other words, an ideal observer using this population of MT cells and a simple averaging scheme for pooling would experience a 14% reduction in perceived speed.

We also performed the analysis shown in Fig. 9 to the subset of significantly adapting cells ($n = 27$). The left and rightward

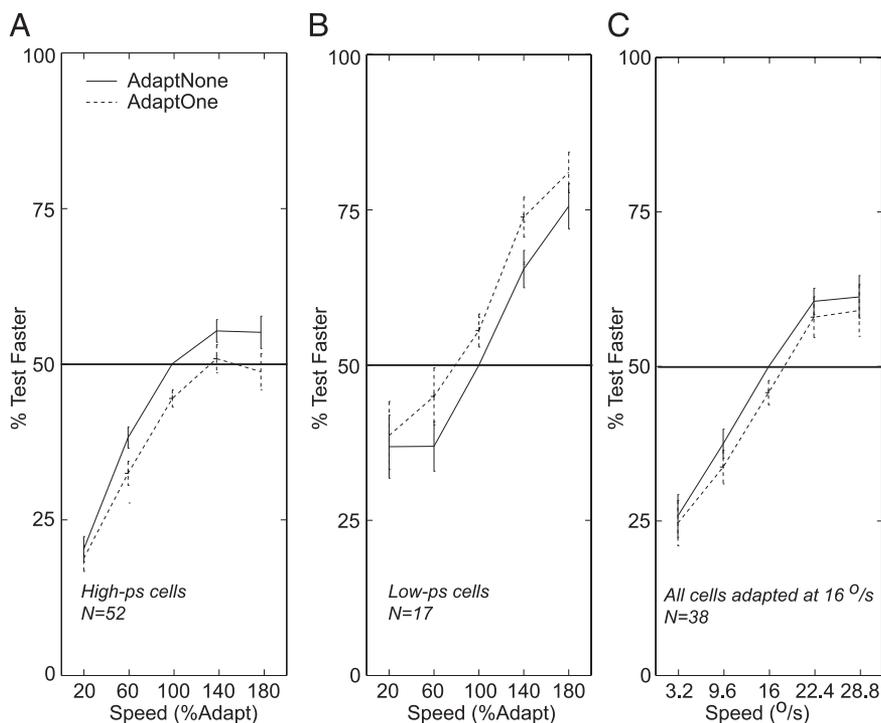


FIG. 9. Average neurometric curves. A: neurometric speed curves averaged over all 52 cells with a preferred speed higher than the reference speed; after adaptation (dashed curve), the curve is shifted to the right of the nonadapted curve (solid curve). B: neurometric speed curve averaged over all 17 cells with a preferred speed lower than the reference speed. C: to compare with behavioral experiments (using adaptation at 16°/s), this panel represents the neurometric curve averaged only over the 38 cells that were adapted at 16°/s. This analysis shows that an ideal observer relying on a single typical cell from these populations would report a decrease in perceived speed after adaptation. This is consistent with the behavioral report of humans and monkeys.

shifts corresponding to those in Fig. 9, A and B, were larger in this subset (74%, $n = 17$; 29%, $n = 10$, respectively). Averaging over all cells that showed significant adaptation effects after adaptation at 16°/s (i.e., the equivalent of Fig. 9C), resulted in a PSE shift of 19%.

Although the speed tuning properties of our population were qualitatively similar to those reported in the literature, it is of interest to know whether this reduction in perceived speed is robust to changes in the composition of the population. In the recorded population, 65% of cells were high-ps cells. By resampling cells (with replacement) independently from the low-ps and high-ps subpopulations, we could simulate populations with different fractions of high-ps cells. In bootstrap fashion, we performed the same analysis used to create Fig. 9C on 1,000 simulated populations of 38 cells with varying compositions. This allowed us to determine the relationship between the shift in PSE (i.e., the change in perceived speed after adaptation) and the high-ps fraction. Over the range of high-ps cell fractions from 10 to 90%, the change in PSE varied almost linearly from -10 to $+30\%$. These numerical values should be interpreted with caution because they depend on the size of the adaptation effects we found in our sample of 38 cells. Qualitatively, however, the result of this analysis shows that a decrease in perceived speed with adaptation occurred as long as the fraction of high-ps cells was $>40\%$.

Adaptation improves discriminability

To determine whether two stimuli are different, an ROC observer need only determine whether the neural responses are different. This avoids the difficulty with interpreting a difference in rates in terms of faster or slower. In other words, modeling of discriminability can be accomplished without assuming a code. We performed ROC analysis to calculate the discriminability for each combination of two speeds in both the adapted and nonadapted state.

Figure 10 shows a scatter plot for all cells of the discriminability before and after adaptation, averaged over all speed comparisons. Most (41/69: 59%) data points fall above the

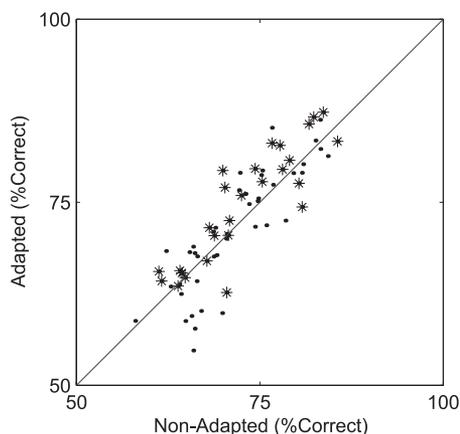


FIG. 10. The improvement of discriminability with adaptation. Scatter plot compares average (over all speeds) discriminability of 2 speeds before adaptation (horizontal axis) and after adaptation (vertical axis). Data points above the diagonal line represent cells in which adaptation improved discriminability. Asterisks refer to cells whose adaptation effects were statistically significant. Graph shows that an ideal observer relying on 1 of these cells would typically perform better at speed discrimination after adaptation.

diagonal line, showing that adaptation typically led to an improved discriminability for speeds in the range ($\pm 80\%$) around the adaptation speed. The median improvement over all cells for all possible speed comparisons was only 0.4% ($P = 0.12$, signed-rank test). The subset of 27 cells that individually showed a significant change in firing rate with adaptation exhibited an average improvement in discriminability of 1.7% per cell ($P < 0.01$, signed-rank test).

To compare the changes in discriminability of the ROC observer with the monkey behavioral experiments (which used the 16°/s adaptation speed), we also applied this analysis to the 38 cells adapted at 16°/s. The median improvement for all possible speed comparisons averaged over these cells was a statistically significant 1.1% ($P < 0.01$, signed-rank test). For the subset of cells ($n = 27$) that showed a significant change in firing with adaptation, the improvement was an even larger 3.5%. Note that this larger improvement is not an automatic consequence of a statistically significant change in firing, because a change in firing could cause either an improvement or impairment in discriminability. For the visual system to make use of this subset, however, it would need to know which cells belong to this group. An alternative view is that with longer adaptation than the 2 s we used in our experiments, many more cells presumably show significant adaptation. If that were the case, the subset of significantly adapting cells in our data may be representative of the improvements that could take place with longer adaptation.

DISCUSSION

Our psychophysical experiments showed that only 2 s of adaptation to a moving stimulus are enough to cause both an underestimation of perceived speed and an enhancement of speed discrimination in both humans and monkeys. Recordings from single cells in macaque MT showed that 2 s of adaptation to a moving stimulus significantly reduced the firing rate to subsequent moving stimuli. We show that the reduction in firing was most pronounced for a different stimulus (speed) than the stimulus (speed) used to adapt the cell. With minimal assumptions about the neural code and an ROC-based ideal observer analysis, we showed that these neural changes are consistent with changes in speed perception and discriminability.

Changes in speed tuning

Our analysis showed that speed adaptation does not lead to a simple reduction in firing. Instead, we found significant changes in the tuning curves. When we quantified those changes with a parametric fit, the changes could be described as a narrowing of the tuning curve. A direct comparison of adaptation effects at different test speeds, however, revealed additional detail on the effects of adaptation. Although there were notable exceptions, the adaptation effect on average increased with the difference between test speed and adaptation speed. To fully study this relationship, a full factorial design in which cells are adapted and tested at many speeds will be required. Such a design may also provide more information on the mechanisms of adaptation. This description of the changes in tuning, however, is enough to reach a qualitative understanding of the perceptual effects. With the assumptions of the

vector average model, a reduction in firing changes the perceived speed, while the narrowing of the tuning curves leads to an enhanced discriminability.

Changes in perceived speed

The neurometric data shown in Fig. 9C suggest that, for the adaptation speeds we studied, perceived speed should be reduced after adaptation. This is indeed the case, both in published psychophysical studies of human speed perception (Goldstein 1957; Thompson 1981) and our own data for humans and monkeys (Fig. 2). Adapting to speeds much lower than the ranges used in this study, however, should preferentially stimulate—and therefore adapt—cells with low preferred speeds and, following Fig. 9B, could thereby induce an *increase* in perceived speed. Such an increased perceived speed after adaptation to very low speeds has indeed been reported for rotational motion (Rapoport 1964). Thompson (1981) argued that the mechanism underlying this increase in perceived speed is contrast adaptation rather than motion adaptation per se. In support of this hypothesis, he adapted at low contrasts and low speeds and tested at high contrasts. Such a low contrast adaptation stimulus does not induce contrast adaptation and, as Thompson showed, does not lead to an increase in perceived speed. Our paradigm only partially controlled for contrast adaptation by using stationary patches of dots in the control conditions. Although these patches have the same average contrast as the moving patches, they do not stimulate identical elements on the retina. Hence, contrast adaptation may at least partially underlie the changes we observed in the neuronal responses to moving stimuli. To disentangle contrast adaptation from direction and speed-specific adaptation, a much more extensive paradigm (e.g., Bex et al. 1999), with adaptation and test stimuli at different contrasts, speeds, and directions would be needed.

Improved speed discriminability

An increased sensitivity to small changes in speed after prolonged viewing of a moving stimulus has been reported previously for human subjects (Bex et al. 1999; Clifford and Langley 1996; Clifford and Wenderoth 1999; Huk et al. 2001). Although our paradigm is somewhat different (we measured an improvement in speed discrimination of 2 stimuli, rather than the ability to detect a small speed change in an ongoing stimulus), our results are similar to the previous findings. Given the constraints of physiological experiments, we only explored the effect of brief (2 s) adaptation to moving stimuli. Longer adaptation may well result in larger perceptual effects. Clifford and Langley, for instance, reported that subjects who were at chance for the detection of a sinusoidal speed modulation before adaptation, performed at nearly 100% after 10 s of adaptation. Moreover, attention and engagement in a task can enhance effects of adaptation (Rezec et al. 2004). Because our monkeys were not performing the speed discrimination task while we recorded the data from MT neurons, it is possible that the observed firing rate changes are smaller than those that would have occurred if the monkey had been performing the task.

Motion adaptation

Previous studies of the neural correlates of motion adaptation in MT have concentrated on changes in directional responses (Kohn and Movshon 2003; Petersen et al. 1985; Van Wezel and Britten 2002). There is consensus that adaptation in the preferred direction of a cell leads to a subsequent reduction in firing rate. Adaptation in the antipreferred direction has led to a more complicated picture. Petersen et al. (1985) showed that long (20 s; in anesthetized monkeys) adaptation in the null direction leads to an enhancement of the response to bars moving in the preferred direction. In a similar adaptation protocol, but using moving gratings, null-direction adaptation was shown to have little effect on the response to the preferred grating, but it did enhance the responses to a flickering grating (Kohn and Movshon 2003). Finally, short (3 s; in awake monkeys) null-direction adaptation to random dot patterns does not generally lead to a change in the response to another moving dot pattern (Van Wezel and Britten 2002). These paradoxical findings suggest that adaptation is not a simple result of neural fatigue but that adaptation interferes with the (opponent) mechanisms that underlie direction selectivity in MT (Krekelberg and Albright 2005). This active interference and the resulting change in directional tuning were shown even more forcefully by a recent experiment by Kohn and Movshon (2004). They used adapting stimuli on the flanks of the directional tuning curve (i.e., nonoptimal directions) and showed that adaptation was weakest at the adapted direction and increased for directions that were different from the adapting stimulus. As a consequence of this direction specific adaptation, the preferred direction of the cell after adaptation was closer to the adapting stimulus. This may explain the changes in perceived direction that occur with adaptation (Levinson and Sekuler 1976). Some of our findings in the speed domain are analogous (e.g., the adaptation effect is largest when tested away from the adaptation speed, see Fig. 5.). However, we found no evidence for a shift in preferred speed with adaptation. (see Fig. 6). Although it is possible that adaptation durations on the order of 40 s would evoke such a shift, this may also be a genuine difference between the representation of speed and direction in MT.

Adaptation in V1

Single-cell adaptation studies in V1 have also revealed a reduction of firing after prolonged exposure to a visual stimulus. In contrast to our finding in MT, in V1 this reduction in firing tends to be largest for a test stimulus that is similar to the adapting stimulus with respect to its spatial frequency (Movshon and Lennie 1979; Saul and Cynader 1989a), temporal frequency (Saul and Cynader 1989b), and orientation (Dragoi et al. 2000, 2001; Felsen et al. 2002; Muller et al. 1999). Such qualitatively different neural changes may be expected to lead to qualitatively different perceptual effects. The changes in perceived direction after adaptation to motion—the direction after-effect—are, however, quite similar to those in the orientation domain—the tilt after-effect (Clifford 2002). It is possible that orientation perception relies on cortical areas downstream from V1, which could have adaptation properties similar to those reported for MT by Kohn and Movshon (2004) and by us. The population coding model proposed by Kohn and

Movshon (2004), however, suggests that, depending on the magnitude of neural adaptation, both V1-like changes in firing (maximum effect for the adapting stimulus) and MT-like changes in firing (maximum effect away from adapting stimulus) can lead to very similar perceptual effects.

Neural code for speed

There is mounting evidence that neurons in MT are related to the perception of speed: the speed tuning of MT cells is form-invariant (Perrone and Thiele 2001; Priebe et al. 2003), lesions of MT reduce speed discrimination performance (Newsome and Pare 1988; Orban et al. 1995; Rudolph and Pasternak 1999), microstimulation of MT changes speed perception (Liu and Newsome 2005), and a large fraction of MT cells shows significant choice probabilities for speed discrimination (Liu and Newsome 2005). These studies, however, do not reveal how the available speed information in MT is used by motor or perceptual systems. In other words, the neural code for speed is still unknown.

To link neural with perceptual data, we made assumptions about this neural code. We believe our assumptions are a minimal set required to relate our behavioral experiments with MT activity. These assumptions allowed us to model ordinal effects of speed perception; we can predict that after adaptation speed should be underestimated, but the size of this effect will depend on many factors. A quantitative comparison of neural and behavioral data are currently out of reach. The reason for this is that one would need to specify in detail how neurons' votes are weighted in the vector average model; such a specification, however, is currently untestable. We nevertheless determined the average perceptual effects expected under the assumptions of our model and found that these are generally of the same order of magnitude as the perceptual effects. For instance, the neural data predict a reduction in perceived speed of 14% for an observer relying on a single average MT cell. The average human subject perceived a reduction of 16.9% and the monkeys perceived a reduction of 5.6%. Similarly, the neural data predicted that for a speed discrimination involving a 16°/s reference speed, an ideal observer relying on a single average MT cell would improve by 1.1%. The human subjects, on average, improved by 3%, whereas monkey M, on average, improved by 6%. Even assuming that MT cells are partially correlated sources of speed information (Shadlen et al. 1996), these behavioral improvements are not out of reach of a mechanism that pools information over MT cells that individually improve by only 1.1%.

One important factor determining the quantitative effects in the model is which subpopulation of MT neurons is actually used for the task. For instance, it is conceivable that neurons are only used for those speed discriminations that involve speeds near the steepest part of their tuning curve. This is clearly related to the results shown in Fig. 7: not every cell is suitable for every speed discrimination and an optimal speed discrimination algorithm would select appropriate cells from the MT population. Purushothaman and Bradley (2005) recently showed that a cell's firing rate variability and the animal's behavior (as measured by the choice probability) are most closely correlated for cells that have steep direction tuning curves near the directions that the animal has to discriminate. On the basis of this, they suggested that the pooling

mechanism for fine perceptual direction discrimination selects cells that are appropriate for the task at hand. For speed perception, Liu and Newsome (2005) recently presented data that support a similar claim. Choice probabilities for speed perception were significantly higher for the subset of cells that were high-pass tuned than those that were band-pass tuned (Liu and Newsome 2005). This fits with the idea shown in Fig. 7 that neurons provide little information for speed discrimination involving speeds near the peaks of their tuning curves. In other words, pooling and selection of cells for a perceptual task does not appear to be random across the whole MT population; the readout mechanism appears to select the appropriate subset for the task at hand.

In conclusion, taken together, our neural and perceptual data suggest that one of the products of speed adaptation may be enhanced sensitivity to the speeds that prevail in the current environment. Functionally, this enhances the relative discriminability of two speeds. A common scenario in which this would be relevant is that of a moving observer. On this observer's retina objects that are stationary or slowly moving in the world move with speeds that may be indiscriminable without adaptation. Enhancing the discriminability of such objects may aid in segmenting separate elements of the environment. Our behavioral results show that this enhancement is found within 2 s; hence even if the observer's speed varies quite rapidly over time, adaptation enhances discriminability. At the same time, however, the absolute speed of the objects is underestimated. This should be detrimental for processes that rely on absolute speed such as, for instance, target interception. Our neural data show that cells in MT may underlie both these perceptual effects. This suggests that MT optimizes the encoding of relative speed at the cost of incorrectly encoding absolute speed. Further studies are needed to understand whether the incorrect absolute estimates of speed are an inevitable consequence of the improved relative judgment, or whether two separate mechanisms, one with the goal to improve discriminability the other with the goal to conserve spikes, lead to these perceptual effects.

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