

Adaptation to Speed in Macaque Middle Temporal and Medial Superior Temporal Areas

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The response of a sensory neuron to an unchanging stimulus typically adapts, showing decreases in response gain that are accompanied by changes in the shape of tuning curves. It remains unclear whether these changes arise purely due to spike rate adaptation within single neurons or whether they are dependent on network interactions between neurons. Further, it is unclear how the timescales of neural and perceptual adaptation are related. To examine this issue, we compared speed tuning of middle temporal (MT) and medial superior temporal neurons in macaque visual cortex after adaptation to two different reference speeds. For 75% of speed-tuned units, adaptation caused significant changes in tuning that could be explained equally well as lateral shifts, vertical gain changes, or both. These tuning changes occurred rapidly, as both neuronal firing rate and Fano factor showed no evidence of changing beyond the first 500 ms after motion onset, and the magnitude of tuning curve changes showed no difference between trials with adaptation durations shorter or longer than 1 s. Importantly, the magnitude of tuning shifts was correlated with the transient-sustained index, which measures a well characterized form of rapid response adaptation in MT, and is likely associated with changes at the level of neuronal networks. Tuning curves changed in a manner that increased neuronal sensitivity around the adapting speed, consistent with improvements in human and macaque psychophysical performance that we observed over the first several hundred ms of adaptation.

Introduction

The brain continually recalibrates to the changing statistics of the environment. One example is the rapid reduction in the firing rate of many sensory neurons when exposed to unchanging stimuli. This “gain adaptation” is often accompanied by “stimulus-selective adaptation,” or changes in a neuron’s sensitivity evident as lateral shifts in its tuning curve. Although these changes may be collectively responsible for driving perceptual changes associated with adaptation, the relative timescales of neuronal and perceptual adaptation are unexplored (Gilbert and Wiesel, 1990; Dragoi et al., 2000; Price and Prescott, 2012). Related to this, adaptation may arise purely at the single neuron level as a result of their spiking history, or at the network level due to interactions between neurons. Typically, stimuli viewed after adaptation appear more different from the adaptor than they really are, with this perceptual repulsion accompanied by improvements in discrimination and detection performance (Gibson and Radner, 1937; Levinson and Sekuler, 1976; Hietanen et al., 2008). Although the perceptual effects of adaptation to moving stimuli are well characterized, the neuronal changes underlying perceptual adapta-

tion have not been explained. The critical cortical areas are likely to be the middle temporal and medial superior temporal (MT/MST) areas, which contain direction-tuned and speed-tuned neurons whose activity has been strongly linked to motion perception (Newsome and Paré, 1988; Salzman et al., 1990; Britten et al., 1996; Price and Born, 2010).

Many studies have examined how adaptation affects a neuron’s preferred stimulus, but these changes may be less relevant for perception than slope changes in the vicinity of the adaptor (Butts and Goldman, 2006). Further, most physiological studies compare pre-adaptation and postadaptation tuning, which risks confounding stimulus-selective adaptation and general gain changes due to contrast adaptation at earlier stages of the visual system. Here we avoided these problems by comparing finely sampled speed tuning curves in macaque MT and MST neurons after adaptation to different speeds, which ensures that contrast adaptation is fixed. Our neuronal data were compared with the performance of macaque and human observers on a speed-change discrimination task. Previous analysis of these data showed that MT/MST activity encodes the sign and timing of changes in stimulus speed, and can be decoded to predict perceptual judgments of monkeys performing the task (Price and Born, 2010). For 75% of speed-tuned units, we observed significant shifts between tuning curves measured after each adapting speed; the shift magnitude was correlated with the transience of a unit’s response, but was not correlated with any aspect of speed tuning. We hypothesize that the tuning shifts reflect a change in network connectivity that may ultimately allow neurons to maintain high sensitivity to small, relative changes in speed, consistent with our observed enhancements in psychophysical speed discrimination performance.

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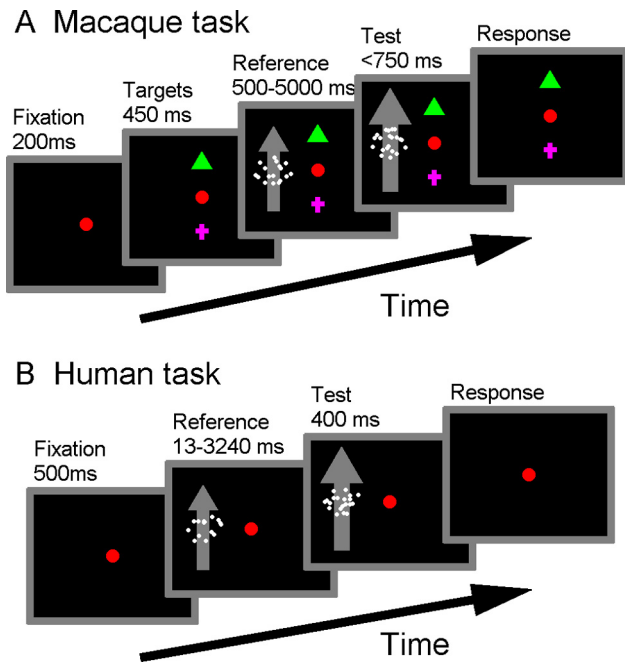


Figure 1. Stimulus and task design. Each black box represents the computer display visible to the subject in the different periods of each task. **A**, Macaque monkeys were trained to perform a speed change task while fixating a central red target. On each trial, 200 ms after acquiring fixation, choice targets (green triangle and magenta cross) appeared for 450 ms, followed by a dot stimulus moving in the preferred direction of the recorded neuron. Speeds during this reference period were 8 or 12%/s. After a random delay of 550–5000 ms the speed abruptly changed to a test speed (4–18%/s). Trials with each adaptation speed, and with speed increments and decrements, were randomly interleaved. Behavioral choices could be made at any time by making a saccadic eye movement to one of the two choice targets, which were presented above and below the fixation target and were visible from the start of each trial. Only correct discrimination choices were rewarded. **B**, Human subjects performed a similar speed change discrimination task while fixating a central target; however, choices were indicated at the end of each trial by keypress. All trials within a block had the same reference duration (13–3240 ms) and test duration (400 ms).

Materials and Methods

The methods and majority of the neuronal dataset were previously described (Price and Born, 2010). Single-unit and multiunit data were recorded from MT and MST in two adult male macaque monkeys (*Macaca mulatta*) weighing 9–11 kg. Each animal was implanted with a custom titanium head-post, a scleral search coil for monitoring eye position and a vertically aligned Cilux recording cylinder (Crist Instruments) to protect a craniotomy centered posterior 3 mm, lateral 15 mm relative to ear bar zero. During recordings, animals were comfortably seated in a primate chair with their head restrained, and were rewarded with juice for fixating a stationary target or correctly performing a speed change discrimination task. All procedures complied with the National Institutes of Health *Guide for Care and Use of Laboratory Animals*, and were approved by the Harvard Medical Area Standing Committee on Animals.

Stimuli and task. Each monkey was trained to perform a speed change discrimination task while fixating a central target (Fig. 1A). On each trial, 650 ms after the animal commenced fixation, a dot stimulus appeared and immediately began moving in the preferred direction of the recorded neuron(s). Speeds during this reference period were 8 or 12%/s. After a random delay of 550–5000 ms (flat hazard function with exponential distribution, $\tau = 550$ –1000 ms) the speed abruptly changed to a test speed. Test-reference speed ratios of 0.5–1.5 were used, giving test speeds of 4–18%/s. Trials with each adaptation speed, and with speed increments and decrements, were randomly interleaved.

The animal was rewarded for correctly indicating whether the stimulus increased or decreased in speed within a window 150–750 ms after the change. Responses were made by making a saccade to one of two choice targets, which were presented above and below the fixation target and

were visible from 200 ms after the onset of fixation. Trials were terminated if the eye position left a square window of 3° side length centered on the fixation target. In addition, a trial was only included in offline analysis if the maximum eye displacement during the reference and test period was <1.5°.

Stimuli were white dots presented on a black screen with resolution 1024 × 768 pixels (17.8 pixels/degree), refresh rate 100 Hz and viewing distance 410 mm. Dots had spatial density 1.5 dots/degree² and 150 ms lifetime, and were restricted to a stationary circular aperture with a diameter that was the smaller of either the excitatory receptive field center of the unit being studied, or the eccentricity of the stimulus center. For each unit we characterized direction tuning while the monkey was rewarded for passively maintaining fixation on a central target. In most neurons, we further characterized speed tuning in the preferred direction using speeds of 0.5–128%/s, which followed 500 ms of a stationary stimulus.

Although we have previously shown that single neuron responses are predictive of the animal's behavioral decisions and reaction times (Price and Born, 2010), similar neuronal responses were observed whether the animal was performing the task or passively fixating, and the outcome of the behavioral task did not significantly affect the tuning discussed here. Therefore, neuronal responses were averaged from all trials regardless of the animal's behavioral response. Further, although psychophysical reports have shown that discrimination performance improves with adaptation duration, these effects are only seen for durations of many seconds (Clifford and Langley, 1996), whereas >85% of our adaptation durations were <2 s. Within the range of reference durations we tested the spiking rate did not change significantly, suggesting that adaptation on this time scale had little effect on speed tuning (see Fig. 4). This is consistent with previous studies on short-term motion adaptation in MT (Priebe et al., 2002). For this reason, responses to trials with the same reference and test speeds were initially pooled, regardless of the adaptation duration.

Electrophysiological recordings. Neurons were assigned to MT or MST based on a range of criteria including: position of the electrode in the chamber judged relative to a postsurgical MRI; electrode depth relative to the dura; size of the spatial receptive field relative to the eccentricity; overlap of the receptive field into the ipsilateral hemisphere; and transitions between gray and white matter as the electrode was advanced (MT was typically encountered at depths beyond MST). In total, we obtained post-adaptation speed-tuning data from 121 single-unit and multiunit isolations, referred to collectively as “units” (see Figs. 3, 6). Sufficient repetitions were obtained in 87 units allowing us to subdivide responses based on adaptation duration (see Fig. 4). Both preadaptation and post-adaptation speed tuning data were obtained from 87 units (see Fig. 5). Note that in the previously published report examining this dataset, a total of 203 units were examined; here we only consider those that displayed significant speed tuning. In monkey N we recorded 79 units (MT: 37 single neurons, 13 multiunit; MST: 22 single neurons, 7 multiunit). In monkey P we recorded 42 units in MT (32 single neurons, 10 multiunit). No qualitative differences were observed between single-neuron and multiunit recordings, or between brain regions or monkeys.

Analysis. Speed tuning during passive fixation was calculated from the average spiking rate 70–170 ms after motion onset (transient response) and 200–500 ms after motion onset (sustained response). Tuning curves were fit with a skewed log Gaussian (Eq. 1) using maximum likelihood methods (Price et al., 2005):

$$R(x) = a \times \exp\left(-\left[\frac{\log(x/x_{\text{pref}})}{b + c \log(x/x_{\text{pref}})}\right]^2\right) + d, \quad (1)$$

where $R(x)$ is the predicted response at speed x /s, x_{pref} is the neuron's preferred speed, a controls the response amplitude, b is the bandwidth, c controls the skew of the curve, and d is the spontaneous firing rate.

Speed tuning during the change discrimination task was calculated separately for trials with each reference speed. Trials were aligned on the time of the speed change, with test responses averaged 50–150 ms after the change and reference responses averaged 0–300 ms before the change. The precise choice of time windows for counting spikes did not

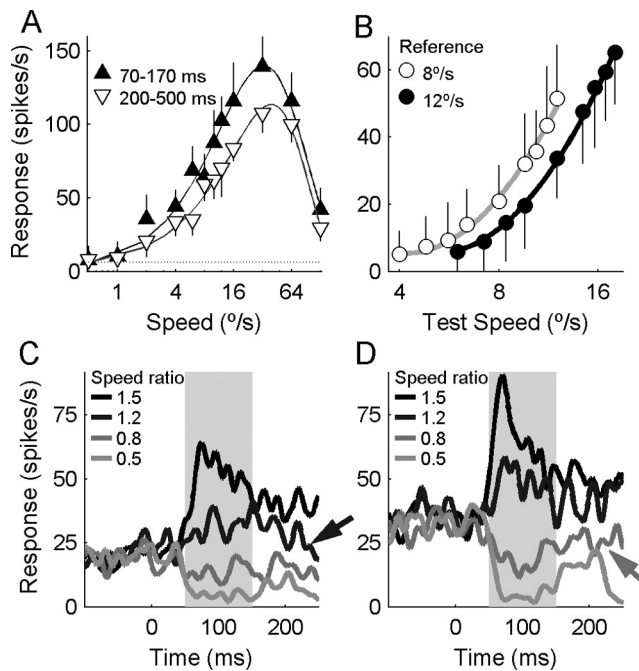


Figure 2. Single neuron speed tuning during passive fixation and speed change task. **A**, Transient (70–170 ms) and sustained (200–500 ms) speed tuning measured during passive fixation. Data points show mean \pm SD. Dashed line is mean spontaneous rate evoked by stationary dots in receptive field. **B**, Speed tuning measured in period 50–150 ms following speed changes from a reference of 8°/s (white circles) and 12°/s (black circles). **C**, **D**, The corresponding spike density functions are shown for stepped speed changes from reference 8°/s (**C**) and 12°/s (**D**), aligned on the time of the speed change. Four different test-reference speed ratios are shown for each reference speed. The shaded gray panel indicates the period 50–150 ms after the speed change which is used to calculate speed tuning following the speed change (**B**). Arrows indicate responses to test speeds of 9.6°/s.

qualitatively affect the results. Any time window in the period 50–250 ms after the speed change produced similar results because this takes into account a neuron's response latency and the behavioral reaction times, which had medians of 250–400 ms depending on the test-reference speed ratio. The chosen 50–150 ms window captures the period when spiking rates are maximally different from the reference period (Fig. 2C,D). The time window used for the reference period was limited so as to exclude the motion onset response from trials with reference durations as short as 550 ms.

Speed tuning curves associated with each reference speed in the discrimination task were separately fit by second order polynomials (median $r^2 = 0.97$). In addition, the two speed tuning curves were fit by a second order polynomial that incorporated either a lateral shift (Eq. 2) or a vertical gain change (Eq. 3) between the responses to the two reference speeds:

$$R(x) = a(x - i \times \delta x)^2 + b(x - i \times \delta x) + c, \quad (2)$$

$$R(x) = (ax^2 + bx + c) \times (gi - i + 1), \quad (3)$$

where R is the predicted response at $x = \log_2(\text{test speed})$; $i = 0$ if the reference was 8°/s and 1 if the reference was 12°/s. Each equation has 4 free parameters: a – c are second order polynomial coefficients; in Equation 2, δx specifies the lateral shift between the responses measured with the two reference speeds; in Equation 3, g specifies the vertical gain change between the two sets of responses. Lateral shifts are expressed in octaves of speed because the function was fitted to the log of test speed.

Speed tuning during the change-discrimination task was judged as significant if one-way ANOVA tests applied separately to the test responses associated with each reference speed indicated significant variation in the mean responses across the range of test speeds ($p < 0.05$). Significance of any lateral shift (Eq. 2) or vertical gain change (Eq. 3)

between the test responses to each reference speed was judged using a likelihood ratio test ($p < 0.05$) to compare the four-parameter fit with a single quadratic function fit to the test responses from both reference speeds.

In 91 of 121 units the four-parameter model incorporating lateral shift parameter δx significantly improved the fits compared with a function in which δx was constrained to be 0 (likelihood ratio test, $p < 0.01$). Similarly, in 88 of 121 units the four-parameter model incorporating the vertical gain parameter g significantly improved the fits compared with a function in which we constrained $g = 1$ (likelihood ratio test, $p < 0.01$). A total of 84 units were better fit by both four-parameter models than the three-parameter, single-quadratic model. To examine whether both lateral shifts and gain changes were required to account for our data, we also examined a six-parameter model. Fits were further improved from the four-parameter model for 30 of 91 units (lateral shift model) and 43 of 88 units (vertical gain model) using the six-parameter model that allowed independent quadratic fits to the responses associated with each reference. This demonstrates that for the majority of cells, the data are equally well described by either gain changes or lateral shifts on their own.

Human psychophysics. Three human participants with corrected refractive errors performed a speed-change discrimination task requiring them to judge whether the test speed at the end of a trial was faster or slower than the reference speed at trial onset (Fig. 1B). The reference period had speed 8 or 12°/s and duration 13, 40, 120, 360, 1080, or 3240 ms. Test periods had a speed of 4.4–17.4°/s and fixed durations of 400 ms. Trials were grouped into blocks of 18–27 trials with the same reference duration, so subjects knew when to expect the speed change. Each subject completed 144–240 trials with each reference duration.

As in the macaque experiments, stimuli were white dots presented on a black screen (resolution 1024 \times 768 pixels; 75 Hz; viewing distance 570 mm), with spatial density 1.5 dots/deg² and 150 ms lifetime. Dots were restricted to a 4-degree diameter aperture, centered 6° to the right of fixation. Head position was stabilized with a chin rest.

Psychophysical data were fit with logistic curves (Eq. 4) using maximum likelihood methods:

$$P(x) = \gamma + (1 - \gamma - \lambda)/(1 + \exp((\alpha - x)/\beta)). \quad (4)$$

Where $P(x)$ is the proportion of trials that were reported to contain a speed increase for a test speed of $x = \log_2(\text{speed})$; α is the point of subjective equality (PSE); β controls the slope; γ and λ control the lower and upper performance plateaus and were constrained to be < 0.05 .

Results

We examined how exposure to closely spaced adapting speeds may reveal subtle shifts in neuronal speed tuning, thus affecting the ability of both neuron and observer to detect and discriminate subsequent changes in speed. We recorded from 121 single-units and multiunits in MT and MST of two rhesus macaques while they viewed adapting stimuli with speeds of either 8 or 12°/s followed by a stepped change to test speeds of 4–18°/s (Fig. 1A). Animals were engaged in a behavioral task requiring the detection and discrimination of speed changes, limiting the range of speed combinations we could present, but allowing direct comparison of neural and perceptual performance (Price and Born, 2010). Units were only included if responses to a minimum of 6 repetitions of each reference test speed combination were recorded. On average, 30 repetitions of each test-reference speed combination were recorded.

Changes in speed tuning after adaptation

Figure 2A shows the speed tuning of a single neuron based on responses during transient (70–170 ms) and sustained (200–500 ms) periods after motion onset, from trials in which the monkey is passively fixating. As is typical for MT neurons, the early, transient response was larger than the subsequent sustained response. This was not attributable to a flash response because the stimulus

was present in the neuron's receptive field for 500 ms before it began moving. The responses of the same neuron to 4 test-reference speed ratios during the speed-change task are shown for reference speeds of 8 and 12°/s, aligned on the time of the speed change (Fig. 2C,D). Because both reference speeds lie on the positively sloped flank of the tuning curve measured during passive fixation (Fig. 2A), increases and decreases in speed led to increases and decreases in firing rate, respectively. Importantly, the amplitude of test responses depended critically on the speed of the reference stimulus. For example, very different responses are observed for the same test speed of 9.6°/s depending on whether it followed an 8 or 12°/s reference (Fig. 2C,D, arrows). Similarly, a test speed of 12°/s following a reference of 8°/s transiently evokes a firing rate that is higher than even the transient response to the onset of the 12°/s reference motion. The transient nature of this response is a signature of neural adaptation, which we explore in more detail below.

To examine the effect of different adaptation conditions on a unit's speed tuning, we measured the mean firing rate during the test period, 50–150 ms after the speed change (Fig. 2B; C and D, gray-shaded region). This fixed time window captures the period when the largest firing rate changes occurred in most neurons. The tuning curves associated with each reference speed are clearly different. Although most units had preferred speeds >12°/s, separation of the two tuning curves was observed for the majority of units, regardless of whether their preferred speed was higher or lower than the reference speeds. Adaptation-induced modulation of tuning may allow these neurons to retain the same qualitative changes in spike rate for speed increments and decrements, regardless of the reference speed.

Casual inspection of shifted tuning curves for single neurons (Figs. 2B, 3A,B) makes it clear that the changes due to reference adaptation can be thought of as either one of, or both, lateral shifts and vertical gain changes. Because we chose to focus on fine sampling of small speed changes around the references, which are more informative about perceptual performance, we were unable to measure the *peak* of the speed tuning curves during the task. Because changes in the location of the peak of the tuning curve are required to distinguish between lateral and vertical shifts, we must remain agnostic about this question—indeed, quantitative models fit to the data indicated that either possibility accounted for our data equally well (See Materials and Methods; median $r^2_{\text{lateral}} = 0.956$; median $r^2_{\text{vertical}} = 0.955$). In terms of neural sensitivity, the critical aspect of the shifts we observed in tuning curves is that they move the steepest part of the tuning curve nearer to the reference speed (Butts and Goldman, 2006). For convenience, we refer to this as a lateral shift, which has the advantage of quantifying the changes in units of the visual stimulus (°/s).

If a neuron's firing rate faithfully encodes absolute speed and adaptation does not change neuronal gain, then we should expect overlapping tuning curves, regardless of the reference speed. This would correspond to a lateral shift of 0°/s (or, in relative terms, 0 octaves). On the other hand, a perfect rescaling of the speed tuning curves such that firing rate encodes the magnitude of relative changes in speed would give two parallel tuning curves laterally shifted by 4°/s, or 0.585 octaves. For the responses to the 8 and 12°/s references, we observed a median lateral shift of 1.6°/s (0.26 octaves) in monkey N and 1°/s (0.17 octaves) in monkey P (Fig. 3C). The median gain change was 1.19 in monkey N and 1.12 in monkey P. Across the neural population, model parameters capturing the magnitude of either the lateral or vertical shift (δx and g , respectively; see Materials and Methods) were strongly corre-

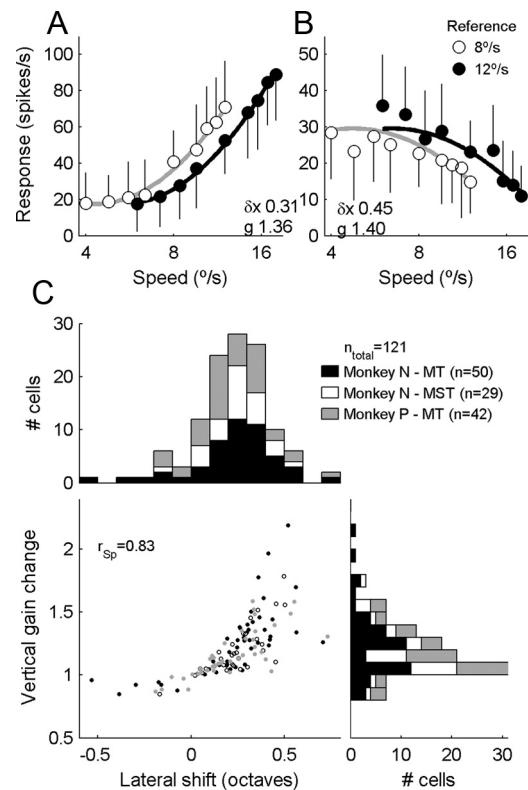


Figure 3. Quantification of changes in speed tuning. **A, B**, Speed tuning of 2 neurons following stepped change in speed from a reference of 8°/s and 12°/s. Solid lines show laterally shifted second order polynomial fitted simultaneously to both datasets. Text in the lower corner of each panel indicates lateral shifts (δx) and vertical gain changes (g) between the two datasets, based on fits of Equations 2 and 3. **C**, Distribution of lateral shifts and vertical gain changes associated with separate fits to the two speed-tuning curves. Data are shown separately for each animal and cortical area. Spearman correlation between lateral shift and vertical gain change was significantly different from 0 for individual animals and areas ($r_{N,MT} = 0.83$; $r_{N,MST} = 0.76$; $r_{P,MT} = 0.80$; $p < 0.01$).

lated, with $r_{\text{Spearman}} = 0.83$ (Fig. 3C). A six-parameter model that separately fits responses associated with each reference speed explained, on average, 93.8% of the variance in the test responses. This represents an increase of only 1.7% compared with the four-parameter models (Eqs. 2, 3), demonstrating that either a lateral shift, or a vertical shift, or both, could account for the changes in speed tuning reported here. There were no significant differences in lateral or vertical shifts between animals or cortical areas (rank-sum test, $p > 0.1$).

Adaptation duration

To render the timing of the speed change unpredictable, the waiting times were drawn from an exponential distribution (see Materials and Methods). This raises a potential problem with the way in which speed-tuning curves were calculated, because the test responses were averaged across a substantial range of reference, or adaptation, durations (550–5000 ms). Despite this, we found little evidence that spiking rate, spiking variability or speed tuning changed over this timescale, suggesting that the relevant changes occurred within the first 550 ms of the adaptation period (Fig. 4). Spiking rate showed a large increase after reference motion onset followed by a subsequent decline, but there was no observable change after 500 ms of motion (Fig. 4A). Similarly, the Fano factor, a measure of neuronal variability, showed a large decrease after motion onset, followed by a small increase, but with little variation after 500 ms (Fig. 4B). This is consistent with

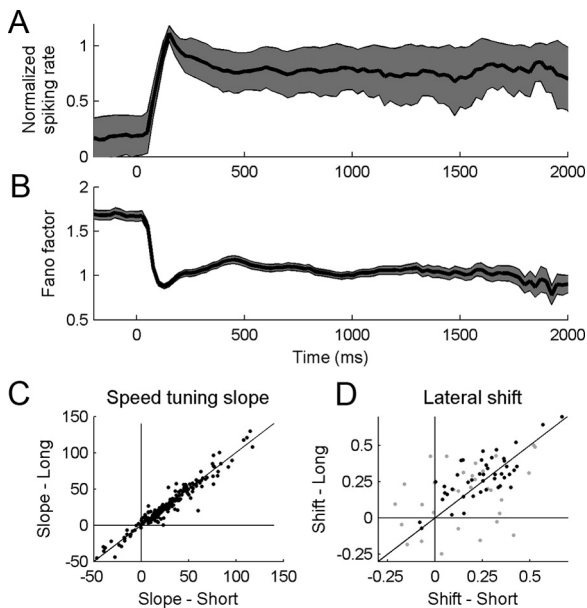


Figure 4. Changes in neural tuning over time. **A, B**, Comparison of mean normalized spiking rate (**A**) and Fano factor (**B**) in sliding 100 ms time windows, shown relative to the onset of reference motion. Shaded regions show mean \pm SEM ($n = 121$). Responses were combined across two animals, both reference speeds and all test speeds. Spiking rates were normalized by subtracting the spontaneous firing rate in the period 200 ms before reference motion onset and scaling to give a normalized peak response of 1 in the first 400 ms of reference motion. **C, D**, Comparison of speed tuning slope and lateral shift calculated separately from Short and Long trials, corresponding to trials with reference durations shorter or longer than 1 s. Only neurons ($n = 87$) with at least 4 trials with each reference test condition in each time window were included. Black data points in (**D**) are those with speed tuning slope > 20 spikes/s/octave.

the initial decrease in trial-to-trial variability after stimulus onset reported previously (Churchland et al., 2010). We compared the spike count and Fano factor in four time windows after motion onset (50–300, 550–800, 1050–1300, and 1550–1800 ms). There were not enough trials to permit an analysis of later time windows. The spike count was significantly higher and Fano factor significantly lower in the earliest time window than all later time windows ($p < 0.01$, one-way ANOVA, with Bonferroni correction for multiple-comparisons).

In 87 units for which we had a sufficient number of trials, we examined how speed tuning during the test period depended on adaptation duration. The slope of quadratic functions fit independently to test responses with each reference speed was not significantly different between trials with short (550–1000 ms) and long (1000–5500 ms) reference durations (Fig. 4C) (t test, $p = 0.97$). Further, there was no significant difference between tuning shifts measured for trials with short and long reference durations (Fig. 4D) (t test, $p_{\text{lateral}} = 0.88$, $p_{\text{vertical}} = 0.11$) and type II linear regression between the data at the two time-points for lateral shift had a slope of 0.98. As neurons with steeper speed tuning slope have a greater dynamic range of spiking responses across the range of test speeds and should give more reliable speed-tuning fits, we separately examined only those 44 units with steep speed tuning slope (> 20 spikes/s/octave of speed). For this subset, the correlation between lateral shift measured in the two time windows was 0.75 ($p < 0.01$). Collectively, these results suggest that there is very little change in tuning beyond 1 s of adaptation.

Tuning changes are unrelated to spike rate adaptation

In an attempt to discover clues to the mechanisms producing the tuning changes, we compared the size of the tuning

changes with a range of parameters derived from each unit's speed tuning measured during passive fixation. We hypothesized that the neurons best suited to provide information about speed changes may display the largest tuning changes. If adaptation primarily depends on the relative effectiveness of the two reference speeds, these would be neurons with preferred speeds distant from the two references but with a large spike-rate modulation over the range of tested speeds. However, the size of tuning changes after adaptation was uncorrelated with preferred speed ($p > 0.05$, data not shown). We calculated the slope of the speed-tuning curve using the derivative of the best fitting skewed log-Gaussian. The absolute value of the slope at the geometric mean of the reference speeds (9.8°/s) was also uncorrelated with the magnitude of tuning curve shifts ($p > 0.05$, data not shown).

If the size of the adaptation-induced change in speed tuning is simply dependent on the firing rate during the reference period, larger changes should occur when there is a greater difference between responses to the two reference speeds. Conversely, to maximize the discriminability of two stimuli near the reference, adaptation could cause greater separation in speed tuning when there is little preadaptation difference in the reference responses. To address this, we calculated two metrics based on the reference responses. The first was a reference response index ($\text{RRI} = (R_{\text{Ref}12} - R_{\text{Ref}8}) / (R_{\text{Ref}12} + R_{\text{Ref}8})$), where R_{Ref} is the mean firing rate during the 300 ms of the reference period before the speed change. Values of RRI close to 1 indicate a large normalized difference between the reference responses; values close to 0 indicate no difference between responses. We found no significant correlation between RRI and lateral shift in tuning curves (Fig. 5A), suggesting that the observed changes in speed tuning are not simply related to the firing rate evoked during the reference period. As a second metric of reference response differences, we calculated the area under the receiver operating characteristic curve (AUROC) for the distributions of responses to the two reference speeds. For completely overlapping response distributions, AUROC takes on a value of 0.5, and as the separation of the two distributions increases, AUROC increases to a maximum value of 1 for completely non-overlapping distributions. Again, there was no significant correlation between AUROC and tuning changes (data not shown, $r_{\text{lateral}} = -0.12$, $p = 0.27$; $r_{\text{vertical}} = 0.05$, $p = 0.64$).

We also compared the size of tuning shifts with a transient-sustained index (TSI), which quantifies the level of response suppression during sustained stimulation. The TSI was calculated from the response to preferred speed motion during passive fixation by comparing the transient response (R_{trans} , 70–170 ms after motion onset) and sustained response (R_{sust} , 200–500 ms after motion onset): $\text{TSI} = (R_{\text{trans}} - R_{\text{sust}}) / (R_{\text{trans}} + R_{\text{sust}})$. A similar metric, the transient-sustained ratio, was previously used to characterize short-term adaptation in MT (Lisberger and Movshon, 1999; Price et al., 2005). The most transient cells had TSI values approaching 1, whereas cells with very little response suppression had TSI values close to 0. The mean TSI was 0.24, indicating that on average the transient response was 63% larger than the sustained response. The TSI was positively correlated with the magnitude of the lateral shift ($r = 0.37$, $p < 0.01$; Fig. 5B) suggesting that similar mechanisms may underlie the two phenomena. These observations are important because previous work characterizing the form of short-term adaptation measured by the TSI has revealed that it is likely to arise via the local circuitry within MT (Priebe et al., 2002).

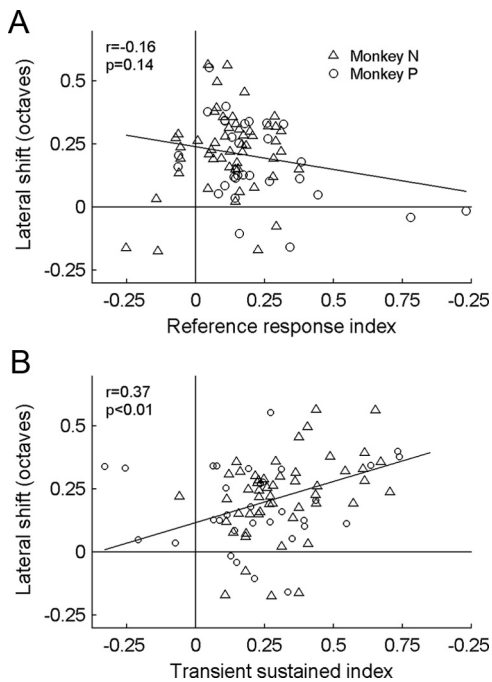


Figure 5. Adaptation induces tuning changes. *A, B*, The size of lateral tuning shifts is compared with the RRI (*A*) and TSI (*B*). The RRI quantifies the difference between the neuronal response to the 8 and 12°/s reference speeds. TSI is a measure of short term adaptation that quantifies the size of the change in the response evoked by the neuron's preferred speed over the first 500 ms of motion. Neurons ($n = 87$) were only included if their speed tuning curve was measured during fixation and was well fit by a skewed log-Gaussian. Diagonal lines, with corresponding r and p values in each panel show the results of linear regression. Only lateral tuning curve shifts showed a significant correlation with TSI. This correlation was significant for neurons from monkey N ($r = 0.44$, $p < 0.01$) but not monkey P ($r = 0.30$, $p = 0.09$).

Absolute versus relative decoding strategies

How do changes in speed tuning affect the information that neurons carry about instantaneous speed and speed changes, and what implications does this have for perception? We can address this issue by determining how well the responses of single neurons can be used to judge the sign of speed changes, whether a decoding neuron only had access to spiking rates during the test (50–150 ms after the speed change) and reference periods (0–300 ms before the speed change). A common way to quantify neurometric performance is the AUROC, which formalizes the level of overlap between distributions of test and reference spiking rates. In calculating AUROC, we took the slope of the speed-tuning curve at the reference speed into account, including whether a change in speed is expected to lead to an increase or decrease in spiking rate. Across all cells, the mean AUROC based on a comparison of the distribution of test spiking rates with the distribution of reference responses from the same trials was 0.74. This was significantly higher ($p < 0.001$) than the mean AUROC based on a comparison of the distribution of test spiking rates with the distribution of all reference trials (0.71). Note that in the latter scenario, test responses are compared with reference responses from trials with both reference speeds. The higher AUROC when test and reference responses from trials with the same speed are compared indicates that perceptually, having information about the reference speed should improve estimates of the sign of the speed change.

A significant problem with ROC-based methods is that they compare two distributions based on spiking rates mea-

sured at two time points in the same trials. Thus, they do not into account temporal correlations, which may lead to firing rates in both test and reference periods of a single trial both being higher or lower than average. To incorporate temporal correlations, we additionally consider three alternative neural decoding scenarios that use the sign of any change in firing rate between the reference and test periods to predict the sign of the speed changes. These neurometric performance calculations do not depend on the mechanisms underlying changes in tuning; they simply use the measured spiking rates to determine how well a given neuron would perform on the task. In the first decoding scenario, each unit's firing rate represents an absolute and memoryless encoding of current stimulus speed, implying it has no knowledge of the prior reference speed or associated firing rate. In this case, to create a binary choice on each trial we compared each test-period response to the average response evoked by both reference speeds. In the second scenario, we assume each unit's firing rate encodes test speed relative to reference speed. This type of decoder can be implemented on a single-trial basis, in which test and reference responses from the same trial are compared, or on an average-trial basis, in which single-trial test responses are compared with the average reference response from the same neuron. In the third scenario, each unit's instantaneous firing rate encodes speed relative to the wrong set of previously seen speeds or firing rates. Good performance on this artificial scenario would constitute strong evidence that adaptation does not benefit neural encoding of the speed changes because the firing rates evoked by the reference period are irrelevant for decoding the sign of the speed change.

In each decoder, if a reference speed is on the positively sloped flank of the unit's speed tuning curve, neurometric performance was the proportion of trials in which increases and decreases in firing rate were associated with increases and decreases in stimulus speed, respectively. Conversely, if the reference speed fell on the negatively sloped flank then neurometric performance was given by the proportion of trials in which increases and decreases in firing rate were associated with decreases and increases in speed.

For both animals, neurometric performance was significantly better (two-sample t test, $p < 0.01$) under the relative decoding strategy than the absolute decoding strategy (Fig. 6*A*). Having access to the matched single-trial reference response for each test response did not improve decoding performance compared with only have the mean reference response (data not shown; t test, $p = 0.29$). Importantly, neurometric performance was significantly better using the relative than the “wrong” strategy (two-sample t test, $p < 0.01$), with a geometric mean improvement of 5.5% (Fig. 6*B*). Although our results do not suggest that a pure “speed-change” signal is present in MT/MST activity, the finding that neurometric performance is highest in the relative encoding scenario demonstrates that discrimination of speed changes using the responses of MT/MST neurons is best when responses to the appropriate reference condition are taken into account.

Temporal changes in behavioral performance

We have demonstrated that adaptation changes a neuron's speed tuning, and that taking these changes into account leads to improved neurometric performance. Thus, it may be expected that the animal's performance should be better on longer trials, which allow for more adaptation. However, within the temporal reso-

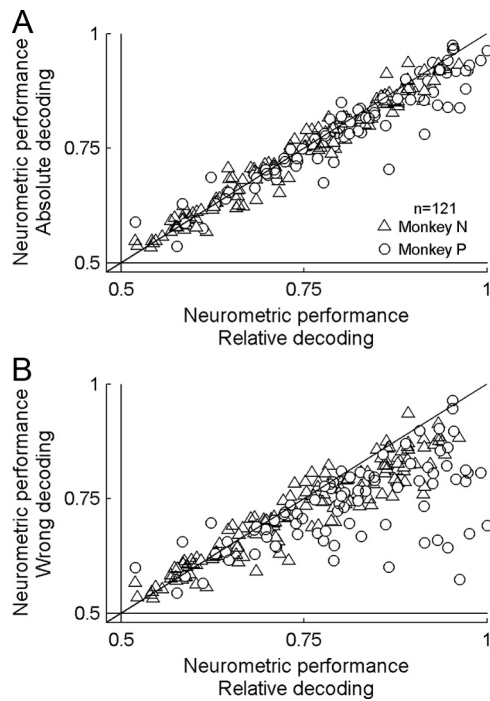


Figure 6. Neural decoding. *A, B*, Comparison of neurometric performance calculated using “Relative” and “Absolute” (*A*) or “Wrong” (*B*) decoding schemes. Neurometric performance is defined as the proportion of trials in which a neuron’s firing rate can be used to correctly discriminate the sign of the speed change. Neurometric performance of 1 represents perfect decoding (every trial is correctly predicted), 0.5 represent chance decoding. With relative decoding, each test response is compared with the mean response evoked by the reference speed presented on that trial. With absolute decoding, each test response is compared with the mean response evoked by both reference speeds. With wrong decoding, each test response is compared with the mean response evoked by the reference speed that was not presented on that trial. For both animals, the relative decoding scheme gives significantly better neurometric performance than either absolute or wrong decoding ($p < 0.01$, t test). No significant differences in performance were found between animals or between areas MT and MST for monkey N ($p > 0.05$, t test).

lution available to us, speed tuning and reference firing rate were not dependent on reference duration (Fig. 4) suggesting that any improvements in behavioral performance might arise only in the first 500 ms of the reference period.

The design of our task for the monkeys did not allow us to test adaptation durations shorter than 550 ms. However, as we suspect that the initial adaptation period dominates the effects on neuronal tuning, we performed a modified psychophysical task in which three human subjects performed a speed change discrimination task with reference durations as short as 13 ms (Fig. 1*B*). Across three participants, we observed a similar dependence of discrimination performance on reference duration: performance improved as reference duration increased from 40 to 360 ms, but beyond that duration, improvements were negligible. To quantify the changes in performance, we fit the psychometric data obtained with each reference duration with a pair of logistic curves constrained to have the same slope (one curve for each reference speed). Typical data are shown for one participant for durations of 120 and 1080 ms (Fig. 7*A, B*). For the shorter duration, the two logistic curves fit separately to the data for each reference speed overlap, indicating that the subject is unable to adequately perform a relative speed judgment. For the longer reference duration, the psychometric curves are well separated, and more importantly, are steeper than with the short reference

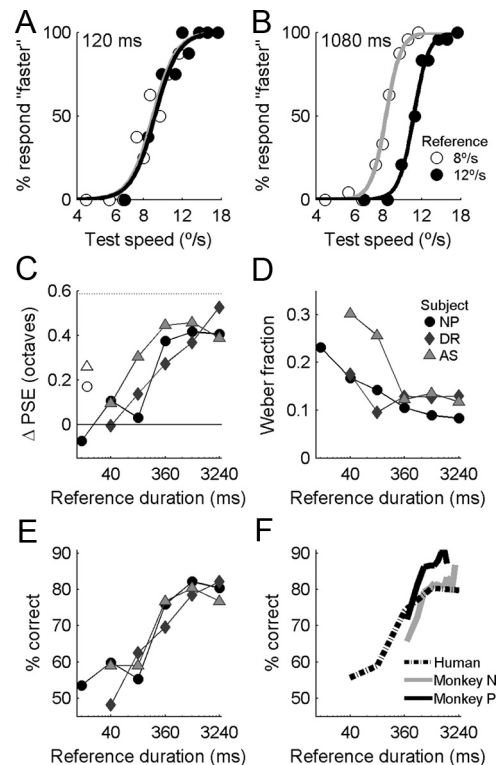


Figure 7. Human psychophysical data. *A, B*, Psychometric tuning functions from subject NP for reference durations of 120 ms (*A*) and 1080 ms (*B*). Fits are logistic curves constrained to have the same slope for the data with each reference speed. *C–E*, Summary metrics for 3 subjects tested with reference durations of 13–3240 ms. With increasing reference duration, the lateral separation in the point of subjective equality (PSE) increased (*C*), the Weber fraction calculated from the 75% threshold in the fitted logistic curves decreased (*D*) and the percentage of correct responses for trials with intermediate test speeds in the range 8–12°/s increased (*E*). Dotted line in (*C*) shows the expected separation of psychometric curves assuming a purely relative response (0.585 octaves). Open markers in *C* indicate the median lateral shift in neuronal tuning curves for monkey N (Δ) and monkey P (\circ). The mean performance of the 3 human subjects is shown overlaid on the performance of the two monkeys (*F*). Reference durations for the monkey experiments were combined using a sliding 200 ms window.

duration, indicating improved discrimination performance (i.e., reduced Weber fractions).

For each duration, we calculated the separation in point of subjective equality (Δ PSE) from the fitted logistic curves. Δ PSE increased with reference duration, and for 2 of 3 subjects, reached a plateau for durations ≥ 360 ms (Fig. 7*C*). For all subjects, the Weber fraction calculated from 75% correct thresholds decreased with reference duration, reaching a plateau for durations ≥ 360 ms (Fig. 7*D*). Finally, from the raw psychophysical data, we calculated the proportion of trials in which the speed change was correctly discriminated, considering only “intermediate” trials in which the test speed was between 8 and 12°/s. The reason for this restricted range is that test speeds < 8 or > 12 °/s can be correctly judged using an absolute strategy, ignoring the reference speed on each trial. For example, a test speed of 14°/s can be correctly judged as “faster” without needing to know the exact reference speed, as long as the subject knows that the reference speeds were only ever 8 or 12°/s. For all subjects, the proportion of correctly discriminated intermediate-speed trials increased almost monotonically from near chance performance to $\sim 80\%$ correct for the longest reference durations (Fig. 7*E*). In combination, these psychophysical results strongly suggest that there is little improvement in discrimination performance for adaptation durations

longer than 360 ms. Finally, in the two monkeys we observed a marked improvement in performance as reference duration increased, which is qualitatively similar to the changes in average human performance (Fig. 7D).

Discussion

Early studies of sensory adaptation characterized it as response suppression after sustained exposure to a stimulus. For most MT neurons, firing rates evoked by constant stimuli decline rapidly over the first 100 ms, and responses to subsequent stimuli are suppressed (Priebe and Lisberger, 2002; Priebe et al., 2002; Price et al., 2005). These gain changes are predominantly attributable to contrast adaptation inherited from the LGN and V1 (Kohn and Movshon, 2003). However, when the confound of contrast adaptation is removed by comparing tuning after different adaptation conditions, conflicting results have emerged. With grating stimuli, direction-tuning curves become narrower and shift toward the adapting direction (Kohn and Movshon, 2004); with dot stimuli, adaptation does not affect direction tuning but preferred speed shifts away from the adaptor (Yang and Lisberger, 2009). These differences have been attributed to the broadband spatial content of dot stimuli, which may produce less adaptation in V1 than gratings (Kohn and Movshon, 2004). It remains unclear whether adaptation-induced changes in MT are entirely inherited from earlier cortical areas, whether they are simply local gain changes that can be predicted from a neuron's previous activation, or whether adaptation is a more complex network-level phenomenon. Here we focus on how and where adaptation-induced changes in speed tuning arise, and the implications of these changes for motion perception.

Our study is the first to reliably observe changes in the responses of MT/MST neurons as a result of adaptation to different speeds. We think this is because we compared tuning curves after adaptation to stimuli that differed only in speed, so contrast adaptation was constant across conditions. Moreover, test speeds were finely sampled (9 speeds >1.6 octaves), whereas previous studies coarsely sampled a larger range, e.g., 5–7 speeds >3–6 octaves (Krekelberg et al., 2006; Yang and Lisberger, 2009). Finally, we tested each neuron with the same adaptation speeds, whereas in earlier studies, the lack of a consistent relationship between a neuron's tuning curve and the adaptation speed may have homogenized any tuning changes (Krekelberg et al., 2006). Thus, we demonstrated that in the majority of speed-tuned neurons in MT/MST, adaptation affects tuning in a manner that improves the ability to discriminate subsequent changes in speed. Our choice of stimuli does present some analytical limitations. Due to the restricted range of test speeds, we cannot distinguish lateral shifts in tuning from vertical gain changes. Further, we did not measure preadaptation and postadaptation speed tuning in identical ways, and therefore cannot distinguish attractive and repulsive lateral shifts. Our stimulus choices were necessitated by the need to present the animals with a challenging task involving stimulus changes of a behaviorally relevant magnitude. Although this precludes completely characterizing each neuron's postadaptation tuning curve, in the context of a discrimination task, it is the ability to identify changes in the tuning curve flanks that is critical for our task (Butts and Goldman, 2006).

Neuronal mechanisms

Three lines of evidence suggest that the changes in speed tuning reported here arise due to a change in network connectivity at the level of MT. First, whereas the dominant feedforward input to MT comes from special complex cells in V1 (Movshon and Newsome, 1996; Perrone and Thiele, 2001; Priebe et al., 2003, 2006; Pack et al., 2006), adaptation in V1 preferentially suppresses responses to the adapted stimulus (Movshon and Lennie, 1979; Saul and Cynader, 1989a, b; Müller et al., 1999; Dragoi et al., 2000; Hietanen et al., 2007). Second, the size of tuning changes was uncorrelated with spiking rates in the reference period, suggesting that a neuron's tuning is affected by more than just its response history. Finally, we showed that maximal tuning changes occurred for adaptation durations as short as 550 ms, and the size of the change in tuning was correlated with a neuron's degree of rapid adaptation (the TSI), suggesting that the two metrics share a common mechanism. Such rapid adaptation in MT is distinct from fatigue or spike-rate adaptation and is equally strong whether the adapting and test stimuli occupy separate or overlapping subregions of the receptive field (Priebe and Lisberger, 2002; Priebe et al., 2002). In combination, these findings suggest that adaptation reflects properties of circuitry within MT rather than in the spatially localized V1 inputs to MT. Further support for a network-level effect would be provided by an examination of changes in response correlations between neurons, as an adaptation-induced reduction in correlated spiking may underlie perceptual improvements in discrimination (Barlow and Földiák, 1989).

Two changes in local MT circuitry might account for the observed changes in speed tuning. One possibility is suggested by models in which recurrent connectivity sharpens broadly tuned inputs (Douglas et al., 1989; Somers et al., 1995; Teich and Qian, 2003). In these models, lateral connection strengths are biased such that excitation is favored between neurons with similar tuning and inhibition is favored between neurons with greater differences in tuning. Decreasing the gain of cells at the adapted location in feature space will remove some excitation from nearby cells. Further, due to sustained inhibition from less adapted cells that prefer stimuli distant from the adapting condition, the cells at the adapted location would display narrowed tuning, or lateral tuning shifts. A second possibility, not exclusive of the first, is that prolonged stimulation preferentially suppresses the tuned inhibitory network, leading to attractive lateral shifts in tuning curves. Although such dynamical changes in the balance of excitation and inhibition have been reported (Heiss et al., 2008), it remains to be explained why different adaptation effects are evident in V1 and MT.

Relationship to perception

Adaptation has two profound effects on motion perception; shifts in perceived direction and speed away from the adapting stimulus (Levinson and Sekuler, 1976; Schrater and Simoncelli, 1998) are accompanied by improved ability to detect and discriminate small changes in speed (Clifford and Langley, 1996; Clifford and Wenderoth, 1999). This suggests that the ability to accurately encode speed in absolute terms may be traded off against improved sensitivity to changes. We have shown here that rapid adaptation affects MT speed tuning in a way that improves change-discrimination performance. Although activity in MT is thought to be causally related to speed perception (Orban et al., 1995; Liu and Newsome, 2005; Price and Born, 2010), it remains to be seen whether adaptation-

induced changes in MT specifically underlie improvements in perceptual discrimination performance. Notably, although a previous study reported that adaptation in MT accounts for changes in perceived speed accompanied by improved neuronal decoding performance on a speed discrimination task specifically after adaptation to 16°/s, when all adaptation speeds were considered no significant improvements in discrimination performance were observed (Krekelberg et al., 2006).

How can we reconcile the timescales of neural changes with improvements in perceptual discrimination performance? Previous studies have shown rapid neuronal and perceptual adaptation on timescales of tens of milliseconds (Priebe et al., 2002; Glasser et al., 2011). Our data suggest that within 1 s of adaptation, MT speed tuning changes to enhance the ability of single neurons to contribute to the detection and discrimination of small changes in speed from the adaptor. In humans, we observed improvements in discrimination performance over similar timescales, with little change in neuronal or perceptual performance over the period 550–5000 ms. In contrast, others have shown that perceptual discrimination improvements continue for up to 30 s (Clifford and Langley, 1996; Kristjánsson, 2001). These results are not inconsistent: the initial rapid change in perceptual performance we observed may be associated with the decay of the neuronal transient response whereas subsequent improvements over tens of seconds may arise due to slower network mechanisms beyond those studied here.

In visual, auditory, and somatosensory systems, adaptation facilitates efficient stimulus encoding of stimulus intensity by matching neuronal sensitivity to the distribution of recent environmental variations (Brenner et al., 2000; Nagel and Doupe, 2006; Maravall et al., 2007). This should increase the discriminability of prevailing stimuli, at the expense of stimuli that occur infrequently. A unifying feature of systems demonstrating efficient stimulus encoding is that the neurons display monotonic tuning; i.e., increased stimulus intensity leads to higher spiking rates. The possibility of adaptation optimizing encoding by neurons with bandpass tuning curves has not been widely investigated (Watkins and Barbour, 2008). Previously, we have shown that changes in response gain can account for the majority of the perceptual effects of direction adaptation (Price and Prescott, 2012). However, improvements in single neuron discrimination of stimuli close to an adaptor can also arise by shifting a neuron's tuning curve so that its flank is centered on the adapting stimulus (Gilbert and Wiesel, 1990). Although such shifts could occur through lateral shifts or gain changes (or both), intuitively, all have the effect of increasing the local slope of the tuning curve. Ultimately, this means that small changes in the stimulus can cause large, rapid changes in neural response, accounting for the rapid changes in perceptual performance reported here.

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