A Logarithmic, Scale-Invariant Representation of Speed in Macaque Middle Temporal Area Accounts for Speed Discrimination Performance

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Human speed discrimination thresholds follow Weber's law over a large range of reference (i.e., pedestal) speeds, that is, the just-noticeable-difference in speed scales in proportion to the reference speed. We analyzed the neural representation of speed information in macaque middle temporal visual area (MT) to determine whether this representation can account for the basic form of psychophysical data. Based on theoretical considerations, we hypothesized: (1) that the speed tuning curves of MT neurons should be bell-shaped (Gaussian) as a function of the logarithm of speed, (2) that the set of speed-tuning curves should be approximately scale-invariant, (3) that the distribution of speed preferences should be approximately uniform in log speed, and (4) that response variability should be independent of speed preference. Our quantitative analysis of data from 501 MT neurons shows that the neural representation of speed approximately obeys these constraints, with modest deviations particularly at slow speeds. We then used the MT data to predict how speed discrimination thresholds should depend on pedestal speed. The shape of this prediction matches very closely to that of human psychophysical data, accounting for constant Weber fractions over a large range of intermediate speeds as well as a marked departure from Weber's law at slow speeds. Moreover, we show that deviations of the MT representation from the above constraints are important for predicting how psychophysical thresholds depart from Weber's law at slow speeds. These findings support the notion that a logarithmic, approximately scale-invariant representation of speed in area MT limits perceptual speed discrimination.

Key words: extrastriate; velocity; MT; population coding; macaque; visual motion

Introduction

The middle temporal visual area (MT) is known to play an important role in motion perception (Albright, 1993; Andersen, 1997). Although most studies of MT neurons have focused on coding of motion direction, it is well established that most MT neurons are also tuned for the speed of motion (Maunsell and Van Essen, 1983; Mikami et al., 1986; Lagae et al., 1993; Churchland and Lisberger, 2001; DeAngelis and Uka, 2003; Liu and Newsome, 2003) and that lesions of MT impair speed discrimination (Pasternak and Merigan, 1994; Orban et al., 1995). It has recently been shown that microstimulation of MT can bias speed perception in monkeys, confirming that MT is important for speed judgments (Liu and Newsome, 2005). However, relatively little attention has been given to the quantitative nature of the

speed representation in MT. It has been noted, for example, that the speed-tuning curves of MT neurons tend to be asymmetric when plotted on linear speed axes (Liu and Newsome, 2003; Priebe et al., 2003), but the functional significance of this observation is not clear. Moreover, the properties of the population code for speed remain unclear.

In human psychophysics, speed discrimination has been studied fairly extensively (McKee and Nakayama, 1984; Orban et al., 1984; McKee et al., 1986; Pasternak, 1987; De Bruyn and Orban, 1988; Watamaniuk and Duchon, 1992). Weber fractions (the ratio of discrimination threshold to reference speed) are approximately constant across pedestal speeds ranging from 5 to 60°/s, whereas they rise markedly at both slower and faster speeds (McKee and Nakayama, 1984; Orban et al., 1984; De Bruyn and Orban, 1988). Presumably, the neuronal substrate for speed discrimination has evolved to support near-constant Weber fractions, because this allows the precision of speed judgments to adjust to the speed of background motion.

If MT contains the neural representation of visual motion that limits speed discrimination, how might the speed-tuning curves of a population of MT neurons be organized to support approximately constant Weber fractions over a wide range of speeds? We hypothesized that Weber-law behavior could be explained in neural terms by a scale-invariant set of speed-

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tuning curves that are bell shaped and uniformly distributed in the logarithm of speed (see Fig. 1A). We verified, using theory and simulations, that this logarithmic coding scheme predicts constant Weber fractions over a large range of speeds. We then studied the representation of speed information in macaque area MT. By analyzing data from 501 neurons, we show that MT approximately satisfies the constraints of the logarithmic coding scheme. Additionally, we show that predicted Weber fractions from our MT population, based on the performance of an optimal unbiased estimator (Seung and Sompolinsky, 1993; Pouget et al., 1998), depend on pedestal speed in a manner that is very closely matched by human psychophysical data.

Our findings suggest that an approximately logarithmic representation of speed in area MT limits perceptual speed discrimination. A preliminary account of our findings has appeared in abstract form (Anderson et al., 2003).

Materials and Methods

Electrophysiology experiments were performed using three adult male rhesus monkeys (*Macaca mulatta*). All data analyzed in this report were collected as part of a previous study (DeAngelis and Uka, 2003), and our experimental methods are described in detail in that publication. Here, we provide a brief summary of our procedures. All experimental procedures were approved by the Animal Studies Committee at Washington University and conformed to National Institutes of Health guidelines.

Surgical preparation. A head restraint post and a recording chamber were attached to the skull using a combination of titanium screws and cranioplastic cement (Plastics One, Roanoke, VA). The recording chamber was aligned in a parasagittal plane, centered 17 mm lateral to the midline and 14 mm dorsal to the occipital ridge. An eye coil was implanted under the conjunctiva of each eye and was sutured to the sclera (7–0 Dexon or 8–0 Nylon).

Visual stimuli and task. Random-dot stimuli were generated by an OpenGL accelerator board (3DLabs GVX1) and presented on a flat-faced 22-inch color monitor (Sony GDM-F500; Sony, Tokyo, Japan) subtending $40 \times 30^\circ$ at a viewing distance of 57 cm. Each dot subtended $\sim 0.1^\circ$, and smooth motion was achieved using hardware anti-aliasing. Stereo half-images for the left and right eyes were presented alternately at a refresh rate of 100 Hz, and stimuli were viewed through ferro-electric shutters (DisplayTech, Longmont, CO) that were synchronized to the video refresh. The 100 Hz refresh rate limited the maximum speed of motion that could be presented. Thus, the vast majority of neurons were tested with a maximum speed of 32°/s, above which coherent motion started to degrade.

In these experiments, monkeys were simply required to maintain fixation on a small ($0.15 \times 0.15^\circ$) yellow spot during the 1.5 s stimulus presentation to obtain a liquid reward. If the monkey's conjugate eye position left the $1.5 \times 1.5^\circ$ fixation window at any time during the stimulus presentation, the trial was aborted and no reward was supplied.

Data acquisition. Tungsten microelectrodes (Frederick Haer Company, Bowdoinham, ME) were introduced into the cortex through a transdural guide tube and typically passed through the anterior bank of the lunete sulcus before entering area MT in the superior temporal sulcus. Raw neural signals from the electrode were amplified, band-pass filtered (500–5000 Hz), and input to a hardware window discriminator (Bak Electronics, Germantown, MD) for single-unit isolation. Only well-isolated single units were studied here. Spike times and behavioral event markers were time stamped with 1 ms resolution and stored to disk. Eye movement signals were sampled at 1 kHz and stored to disk at 250 Hz.

Experimental protocol. After isolating action potentials from a single unit, the receptive field (RF) properties were explored using a mouse-controlled RF mapping program. After RF location, RF size, preferred velocity, and disparity were estimated, each neuron underwent an iden-

tical series of quantitative tuning measurements. This series consisted of a direction-tuning curve, a speed-tuning curve, a size-tuning curve, and a horizontal disparity-tuning curve. Because these measurements are described previously (DeAngelis and Uka, 2003), and because this study focuses on speed selectivity, we will only consider the speed-tuning protocol further.

To measure a speed-tuning curve, each neuron was tested with random-dot patterns having speeds of 0, 0.5, 1, 2, 4, 8, 16, and 32°/s. A handful of neurons preferring faster speeds were also tested with 64°/s although coherent motion was slightly degraded at this speed. Stimulus direction, size, and disparity were set to the optimal values for each neuron. Each different speed was presented three to seven times in block-randomized manner.

Data analysis. A single-trial response was computed as the mean firing rate over the 1.5 s stimulus duration. Speed-tuning curves were constructed by plotting the mean firing rate ($\pm$ SE) as a function of stimulus speed (see Fig. 2A).

Speed-tuning curves were fit with various functions (as described below) using the constrained minimization tool, "fmincon," in Matlab (MathWorks, Natick, MA). The best fit of each function was obtained by minimizing the sum-squared error between neuronal responses and function values. Two aspects of this fitting process are worth noting. First, we fit all of the single-trial responses of the neuron, not just the mean response. This allowed us to evaluate the quality of the fit using a χ^2 goodness-of-fit test (DeAngelis and Uka, 2003). Second, we fit the square root of the function to the square root of the data, because this operation helps to homogenize the variance of the neuronal responses (Prince et al., 2002a).

Results

Speed-tuning curves were analyzed for a population of 501 MT neurons recorded from three monkeys (230 units from monkey B; 166 units from monkey J; 105 units from monkey R). These data were collected as part of another study (DeAngelis and Uka, 2003). There were no specific criteria for including a neuron in this sample; we recorded from every neuron that we could activate with random-dot stimuli over the range of speeds that we could test (in searching for neurons, speeds up to $\sim 50^\circ$ /s were commonly tested). We may not have recorded from neurons that only responded to very fast speeds, but we estimate that, at most, 10–20% of neurons were passed over on these grounds (Palanca and DeAngelis, 2003).

Coding schemes and predictions

Before examining the neuronal data, we first considered how the speed-tuning curves of a population of MT neurons might be organized to produce speed discrimination performance that obeys Weber's law. Figure 1 illustrates the predicted behavior of idealized logarithmic and linear coding schemes. Although these are just two of many possible coding schemes, they provide some intuition as well as a set of predictions to examine.

The logarithmic coding scheme shown in Figure 1A is a very efficient way to obtain Weber-law behavior with a small number of neurons (see Discussion). This scheme has four basic features: (1) the individual units have speed-tuning curves that are bell-shaped in log speed (i.e., log-Gaussian); (2) all units have the same shape and width of tuning in log speed, which means that they form a scale-invariant set; (3) speed preferences are uniformly distributed in log speed; and (4) the variability of neural responses is independent of speed preference. One can evaluate the expected performance of such a coding scheme by computing the variance of an optimal, unbiased estimator based on these neurons (Seung and Sompolinsky, 1993; Pouget et al., 1998) (discussed further

Figure 1. Two potential schemes for population coding of speed in area MT. **A**, The logarithmic coding scheme. Here, response is plotted as a function of speed (on a log axis) for 10 idealized units (color coded). In this scheme, each unit has Gaussian tuning in log speed with a fixed log bandwidth. Speed preferences are distributed uniformly in log speed. **B**, The logarithmic scheme predicts that speed discrimination thresholds (black line) should increase linearly with reference (i.e., pedestal) speed, and that Weber fractions (red line) should be constant. Deviations from this idealized behavior at the edges of the plot are a boundary effect attributable to the fact that tuning curves cease to overlap normally at the edges of the coding range. **C**, The linear coding scheme. In this case, each unit has Gaussian tuning for speed (on a linear axis), and speed preferences are distributed uniformly along the linear axis. **D**, The linear scheme predicts that speed discrimination thresholds (black line) should be constant, such that Weber fractions decline markedly with increasing pedestal speed (red line). deg/sec, Degrees per second.

below). Figure 1B (black line) shows that the threshold performance of an optimal estimator increases as a linear function of log speed. As a result, the Weber fraction is constant over most of the range of speeds covered by this group of units (Fig. 1B, red curve). If the speed tuning of MT neurons approximately matches this logarithmic coding scheme, then MT might account for the psychophysical dependence of speed discrimination thresholds on pedestal speed (McKee and Nakayama, 1984; De Bruyn and Orban, 1988). In the Appendix, we present a mathematical description of the conditions under which performance of an optimal estimator will obey Weber's law, and we demonstrate that these conditions are consistent with the logarithmic coding scheme.

In contrast, Figure 1, C and D, shows that a linear speed-coding scheme will not achieve the result expected from psychophysics. In this scheme, units have Gaussian tuning, equal variance, and a uniform distribution of preferences on a linear speed axis (Fig. 1C). As a result, the threshold performance of the optimal estimator is constant as a function of speed (Fig. 1D, black line), and the Weber fraction declines steadily with increasing pedestal speed (Fig. 1D, red line).

With these two potential coding schemes as a backdrop, we now examine the shape and distribution of speed-tuning curves in area MT.

Shape of speed-tuning curves in MT

Figure 2A shows speed-tuning curves from four representative MT neurons having speed preferences of ~1, 4, 8, and 16°/s. These data are plotted on a linear speed axis, and it is clear that

MT speed-tuning curves are not symmetrical (i.e., bell-shaped) in this domain. Rather, responses rise rapidly with increasing speed at the low-speed end of the curve and fall much more gradually as speed continues to increase past the preferred value of the neuron. Figure 2B shows the same data plotted on a logarithmic speed axis. In this case, the tuning curves look approximately bell-shaped (i.e., Gaussian), as also observed in previous studies (Liu and Newsome, 2003; Priebe et al., 2003; Priebe and Lisberger, 2004; Pack et al., 2005). This suggests that speed is coded logarithmically in MT.

To test this idea quantitatively, we fit MT tuning curves with three different functions: a Gamma function, a log Gaussian, and a standard Gaussian. We previously used the Gamma function to fit the speed-tuning curves of MT neurons, and we found that it provides excellent fits (DeAngelis and Uka, 2003). Specifically, the median R^2 value of the Gamma fits was 0.979, and 80% of neurons passed a stringent χ^2 goodness-of-fit test ($p > 0.05$). The Gamma function is formulated as follows:

$$R(s) = R_0 + A \times \frac{[\alpha(s - \tau)]^n \times \exp[-\alpha(s - \tau)]}{n^n \times \exp(-n)}, \quad (1)$$

where R_0 , A , α , τ , and n are free parameters. Parameters R_0 and A determine the baseline firing rate and depth of modulation, respectively, whereas α , τ , and n determine the shape and location of the function. As the exponent n increases, the Gamma function takes on a range of shapes from exponential to log-Gaussian to Gaussian, making it very flexible for capturing the diversity in shapes of speed-tuning functions that we observed (DeAngelis and Uka, 2003; Palanca and DeAngelis, 2003). The solid curve in Figure 3A shows the fit of a Gamma function to the speed-tuning curve of an example MT neuron.

In the present study, we also fit MT speed-tuning curves with a log-Gaussian function described by the following:

$$R(s) = R_0 + A \times \exp\left[-\frac{\log[q(s)]^2}{2\sigma^2}\right], \quad (2)$$

$$\text{where } q(s) = \frac{s + s_0}{s_p + s_0}, \quad (3)$$

and R_0 , A , s_0 , s_p , and σ are free parameters. The preferred speed is given by s_p , and σ determines the width of the curve (in log speed). Note that the offset parameter, s_0 , is necessary to keep the logarithm from becoming undefined as stimulus speed approaches zero. The dashed curve in Figure 3A shows the best log-Gaussian fit to data from the example neuron.

Figure 2. *A*, Speed-tuning curves of four typical MT neurons, plotted on a linear speed axis. Each curve shows the mean ($\pm$ SE) response of the neuron as a function of stimulus speed, and responses have been normalized so that the peak response of each neuron is equal to 1.0. *B*, Speed-tuning data from the same four MT neurons, plotted on a logarithmic speed axis. Note that the curves are approximately bell shaped in log speed. deg/sec, Degrees per second.

Finally, we also fitted the speed-tuning curves of MT neurons with a standard Gaussian function given by the following:

$$R(s) = R_0 + A \times \exp\left[-\frac{(s - s_p)^2}{2\sigma^2}\right], \quad (4)$$

where R_0 , A , s_p , and σ are free parameters. Because this function is bell-shaped on a linear speed axis (as in the scheme of Fig. 1C), it does not provide a satisfactory fit to the data of the example neuron in Figure 3A (dot-dashed curve).

The neuron in Figure 3A is typical of most MT neurons in that both the Gamma and log-Gaussian models provide excellent fits to the data (R^2 values are 0.978 for the Gamma model and 0.964 for the log-Gaussian), whereas the Gaussian model achieves an R^2 value of only 0.803. Similar results for the whole population of neurons are summarized in Figure 3, B and C. In Figure 3B, the R^2 value for the Gamma function model is plotted against the R^2 value for the log-Gaussian model for each neuron. Median values of R^2 are 0.979 for the Gamma model and 0.968 for the log-Gaussian (note that these values are nearly identical to those for the example neuron in Fig. 3A). Clearly, both of these models fit the speed-tuning curves of MT neurons very well [a similar result for the log-Gaussian model was recently reported by Pack et al. (2005)]. Nevertheless, it can be seen that the majority of the data points in Figure 3B lie above the unity-slope diagonal, and the difference in median R^2 value between the two models is statistically significant (Wilcoxon matched pairs test; $Z = 10.15$; $p < 0.0001$; $n = 501$). Thus, although the log-Gaussian function is a very good model for speed tuning in MT, the Gamma function model is slightly superior. We shall further evaluate the origin and impact of this small difference later.

Figure 3C compares R^2 values obtained from fits to the Gaussian and log-Gaussian models. The median R^2 value for Gaussian fits (0.791) is considerably lower than the median value (0.968) for the log-Gaussian fits, and this difference is highly significant (Wilcoxon matched pairs test; $Z = 19.1$; $p \ll 0.0001$; $n = 501$). Moreover, 70% of MT neurons pass a χ^2 goodness-of-fit test ($p > 0.05$) for the log-Gaussian model, but only 22% of neurons pass this test for the Gaussian model. Thus, it is clear that the speed-tuning curves of MT neurons are better described as bell shaped functions of log speed than linear speed. Moreover, the log-Gaussian model provides a good characterization of the data for the vast majority of neurons, consistent with the coding scheme in Figure 1A.

Scale-invariance of speed tuning in MT

Having established that the speed-tuning curves of MT neurons are well described by a log-Gaussian function, we now

address whether the tuning curves of a population of MT neurons form a scale-invariant set. Speed would be coded in a scale-invariant manner if the normalized tuning curves of all MT neurons had the same shape but were simply shifted horizontally along the log-speed axis (as is approximately true for the example neurons in Fig. 2B). The two parameters of the log-Gaussian model that determine the shape of the speed-tuning curve are s_0 and σ , and the logarithmic coding scheme of Figure 1A predicts that these parameters should be independent of speed preference. We now examine the distributions of these parameters across our population of MT neurons, how they vary with speed preference, and how fixing these parameters affects the quality of fits to our tuning curves. Note that, strictly speaking, a set of MT speed-tuning curves can only be scale invariant if s_0 is equal to zero (Eqs. 2, 3); thus, we also wanted to examine the values of s_0 .

Figure 4A (right) shows the distribution of the speed-tuning width parameter, σ . Values of this parameter lie mainly between 0 and 3.0, with a mode close to one (median, 1.16). Note that σ is a unitless quantity because of the formulation of $q(s)$ in Equation 3. Most of the distribution of σ lies within a spread of two octaves. The scatter plot in Figure 4A shows that σ does not depend substantially on the preferred speed of the MT neurons. There is only a very weak negative correlation (Spearman rank correlation; $r = -0.11$) between σ and speed preference, and this correlation is of marginal significance ($p = 0.028$). Figure 4B shows the distribution of the other tuning shape parameter, s_0 . This parameter typically takes on values close to zero, but the distribution has a long positive tail, such that some neurons have s_0 values substantially larger than zero. The median value is 0.33°/s. The scatter plot in Figure 4B shows that s_0 has little dependence on speed preference, with only a marginal positive correlation ($r = 0.10$; $p = 0.035$). Although there is substantial scatter in the distributions of σ and s_0 , these parameters are approximately independent of speed preference as expected in the logarithmic coding scheme.

From the data in Figure 4, it is difficult to assess directly how much the population of MT neurons deviates from coding speed in a scale-invariant manner. To address this question more directly, we again fitted the data from each MT neuron with two different models: a log-Gaussian model with all parameters free (as described above) and a log-Gaussian model with σ and s_0 constrained to the median values measured across the population. This constrained log-Gaussian model has two fewer parameters than the free log-Gaussian model.

Results of this analysis are shown in Figure 5, where the R^2 value for the free model is plotted against the R^2 value for the constrained model. Fixing σ and s_0 reduces the median R^2 value from 0.968 to 0.922 (a 4% reduction in explained variance); however, the data from most cells are still well fit by the constrained model. Moreover, the fits of the constrained log-Gaussian model (three free parameters) are still significantly better overall than the fits of the linear Gaussian model (Eq. 4) (Fig. 2C) with four free parameters (Wilcoxon matched pairs test; $Z = 13.9$; $p \ll 0.0001$; $n = 501$). The insets in Figure 5 show curve fits for three neurons that span the range of the data. To summarize the effect of fixing σ and s_0 , we compared the errors associated with the two log-Gaussian models using a sequential F test (Draper and Smith, 1966; Prince et al., 2002b; Palanca and DeAngelis, 2003), which accounts for the difference in degrees of freedom between the two models. Using this test, we can determine whether each MT neuron was signifi-

Figure 3. Comparison of Gamma, log-Gaussian, and Gaussian fits to MT speed-tuning curves. **A**, Speed-tuning data are shown for an example MT neuron (filled symbols), along with the best fits of the Gamma function model (solid line), the log-Gaussian model (dashed line), and the Gaussian model (dot-dashed line). The thin dotted line denotes spontaneous activity level. **B**, Population data showing the R^2 value of the Gamma fit plotted against the R^2 value of the log-Gaussian fit for each MT neuron studied ($n = 501$). Median R^2 values are 0.979 and 0.968 for the Gamma and log-Gaussian models, respectively. The diagonal identity line has a unity slope. **C**, Population data showing the R^2 value of the Gaussian fit plotted against the R^2 value of the log-Gaussian fit. Median R^2 values are 0.791 and 0.968 for the Gaussian and log-Gaussian models, respectively. Note that the y-axis scale has been enlarged relative to that in **B**. deg/sec, Degrees per second.

Figure 4. Distributions of shape parameters of the log-Gaussian fit to MT speed-tuning curves. **A**, The speed-tuning width parameter, σ , is plotted as a function of preferred speed for our sample of MT neurons. The histogram to the right shows the marginal distribution of σ ; the median value is 1.16. **B**, The speed offset parameter, s_0 , is plotted as a function of speed preference, with marginal distribution shown by the histogram to the right. The median value of s_0 is 0.33. deg/sec, Degrees per second.

cantly better fit by the free log-Gaussian model than by the constrained model. Because the sequential F test is strictly applicable only to functions that are linear in their parameters, we performed Monte Carlo simulations to confirm that our computed F values followed an F distribution with the appropriate degrees of freedom, such that the test had an appropriate rejection rate (Prince et al., 2002b; Palanca and DeAngelis, 2003).

Among our sample of neurons, 197 were better fit by the free log-Gaussian model (sequential F test; $p < 0.05$) (Fig. 5, filled symbols), whereas 303 were equally well fit by the constrained model ($p > 0.05$; open symbols). In other words, the tuning of $\sim 60\%$ of MT neurons is consistent with a scale-invariant code for speed. Moreover, many other neurons show only modest deviations from scale invariance. The result of Figure 5 changes little if s_0 is fixed to a value much closer to zero (0.001); this reduces the median R^2 value to 0.906.

To further compare the constrained and free log-Gaussian models, we computed the Akaike Information Criterion with correction for small sample size (AICc). The model with the lower value of AICc is considered to be a more parsimonious description of the data (Burnham and Anderson, 2002). Among our sample of MT neurons, 71% had smaller AICc values for the constrained log-Gaussian model than the free model, and the average AICc for the constrained model was significantly smaller than the average AICc for the free model (paired t test; $p \ll 0.001$). This further supports the idea that

a scale-invariant set of log-Gaussian functions (fixed σ and s_0) provides a reasonable approximation to the family of speed-tuning curves in area MT. Although there is considerable scatter in the distribution of shape parameters of the free log-Gaussian model (σ and s_0), fixing these parameters still provides a reasonable approximation to the data, because they do not depend strongly on speed preference (Fig. 4).

Departures from log-Gaussian behavior at slow speeds

The data of Figure 3B showed that the Gamma function model was slightly superior to the (free) log-Gaussian model. Here, we demonstrate that the source of this difference is a systematic error in the quality of log-Gaussian fits for neurons

that prefer slow speeds.

Figure 6, A and C, shows data from two MT neurons that responded maximally to a speed of $0.5^\circ/\text{s}$ and that gave almost equally strong responses to stationary stimuli ($0^\circ/\text{s}$). We described these types of neurons in MT previously (Palanca and DeAngelis, 2003). Solid curves in these graphs show the best fits of the log-Gaussian model to the filled data points. Extrapolating these log-Gaussian fits to negative speeds (which represent motion in the antipreferred direction), we see that the log-Gaussian fits predict relatively weak direction selectivity for these neurons. In contrast, Figure 6, B and D, shows direction-tuning curves for the same two neurons (measured at a speed of $0.5^\circ/\text{s}$), and it is clear that both neurons exhibit robust direction tuning. The response of each neuron to antipreferred motion at $0.5^\circ/\text{s}$ is shown by the unfilled symbol in both the direction and speed-tuning curves. Clearly, the log-Gaussian fit does not fall off quickly enough at low speeds to accommodate this data point.

Whereas the log-Gaussian model predicts that direction selectivity should be poorer for neurons that prefer slow speeds, we found no tendency for this to be the case in our sample of MT neurons. Figure 7A plots the direction modulation index (DMI) of each MT neuron as a function of preferred speed. DMI is defined as follows:

$$\text{direction modulation index} = \frac{R_{\max} - R_{\min}}{R_{\max} - S}, \quad (5)$$

where $R_{\max}$ is the maximum response in the direction-tuning curve, $R_{\min}$ is the minimum response, and S denotes the level of spontaneous activity. We found a weak but significant negative correlation between DMI and preferred speed ($r = -0.15$; $p < 0.001$), whereas the log-Gaussian model predicts a positive correlation.

Figure 7B shows that the superiority of the Gamma model over the log-Gaussian model is confined to neurons that prefer slow speeds. In this graph, the ratio of R^2 values for the Gamma and log-Gaussian models is plotted as a function of preferred speed. Ratios larger than unity indicate better fits of the Gamma function model, and it is clear that this mainly occurs for neurons tuned to slow speeds. Among neurons with speed preferences $< 10^\circ/\text{s}$, the average ratio of R^2 values is significantly larger than unity (t test; $p \ll 0.001$). For these units, the Gamma model is able to rise more steeply with

Figure 5. Evaluation of scale-invariance of speed tuning in MT. In the central scatter plot, the R^2 value of the standard log-Gaussian (Log-Gauss) fit (with all parameters free) is plotted against the R^2 value for a log-Gaussian fit in which both σ and s_0 are fixed to their median values across the MT population. Filled symbols denote neurons for which the unconstrained log-Gaussian model (free σ and s_0) provides a significantly better fit than the constrained model ($p < 0.05$; sequential F test). Unfilled symbols denote neurons for which the constrained model is not significantly worse than the unconstrained model ($p > 0.05$); these neurons can be said to conform to scale invariance. Insets, Speed-tuning data, along with best fits of the constrained and unconstrained log-Gaussian models, are shown for three example neurons that illustrate the range of the data. The format of each inset graph is analogous to that of Figure 3A. deg/sec, Degrees per second; spikes/sec, spikes per second.

increasing speed and thus provides a better fit to the data at the low-speed end of the curve. As described later, this deviation of tuning-curve shape from log-Gaussian makes a modest contribution to the departure of discrimination performance from Weber's law at slow speeds.

Evaluating other constraints of the logarithmic coding model

Thus far, we have shown that speed-tuning curves of MT neurons are well described by a log Gaussian model and that the tuning curves of the population form an approximate, but certainly not perfect, scale-invariant set. We now evaluate the remaining features of the logarithmic coding scheme illustrated in Figure 1A. We examine whether the distribution of speed preferences is uniform in log speed, and we assess whether the variability of neuronal responses is independent of preferred speed.

Figure 8A shows the distribution of speed preferences for our MT population, plotted on a linear speed axis. With these equal-size speed bins, it is clear that the distribution of speed preferences is heavily biased toward slow speeds. Approximately half of the neurons prefer speeds between 0 and 7°/s. This distribution is approximately consistent with other studies of MT neurons that have used random-dot patterns as stimuli (Churchland and Lisberger, 2001; Liu and Newsome, 2003; Palanca and DeAngelis, 2003; Priebe et al., 2003; Pack et al., 2005), and some differences between studies could be attributable to stimulus parameters such as contrast (Pack et al., 2005). Figure 8B shows the same data replotted using speed bins that are one octave in size. Plotted this way, the distribution of speed preferences is much flatter, although there are

Figure 6. Examples of log-Gaussian fits for two MT neurons tuned to very slow speeds. **A, C**, Speed-tuning curves are shown for two neurons that responded maximally to a speed of 0.5°/s. Solid lines show the best fits of the unconstrained log-Gaussian model to the filled data points. The unfilled data point shows the response of the neuron to motion at 0.5°/s in the antipreferred direction. **B, D**, Direction-tuning curves for the same two MT neurons, measured at a speed of 0.5°/s. Filled symbols show mean responses ($\pm$ SE) to eight directions of motion, 45° apart, and the solid lines are the best fits of a Gaussian function. Note that both neurons are strongly direction tuned, which would not be predicted from the log-Gaussian fits to speed tuning. deg/sec, Degrees per second.

fewer neurons at low speeds than would be expected based on a uniform distribution in log speed. Nevertheless, the distribution of speed preferences in MT is at least approximately consistent with the prediction of the logarithmic coding scheme (Fig. 1A).

Figure 8C examines the relationship between response variability and speed preference. For each neuron, we computed the mean and variance of firing rate at each tested speed. In Figure 8C, the average variance/mean ratio (averaged across speeds) of each neuron is plotted as a function of its preferred speed. There is no correlation between these variables ($r = 0.03$; $p = 0.51$), indicating that response variability does not depend on preferred speed.

The logarithmic coding scheme illustrated in Figure 1A assumes that all tuning curves have the same amplitude; thus, an effective assumption of this scheme is that response amplitude does not depend on speed preference. To evaluate this assumption, we examined the amplitude of the Gamma fits to our speed-tuning curves (Eq. 1, parameter A). Tuning-curve amplitude had a mean value of 67.6 spikes/s (± 2.2 SE), but there was no significant correlation between amplitude and speed preference ($r = 0.07$; $p = 0.11$) across the population. Thus, the assumption that response amplitude is independent of speed preference seems valid.

Overall, the data from MT approximately, but not perfectly, satisfy the constraints of the logarithmic coding scheme illustrated in Figure 1A. We thus predict that the population of MT neurons would support an approximately constant Weber fraction over most of the speed range that we tested, with some expected deviation at low speeds for which MT neurons depart most strongly from the idealized log-coding scheme.

Population prediction of speed discrimination thresholds

To examine more directly whether the population of MT neurons can account for speed discrimination observed psycho-

Figure 7. Population analysis of direction selectivity and its relationship to the log-Gaussian model of speed tuning. **A**, The DMI for each MT neuron is plotted as a function of its preferred speed. The preferred speed for each neuron was derived from the peak of the best-fitting Gamma function. There is no tendency for neurons tuned to slow speeds to be less direction selective than neurons tuned to faster speeds. **B**, The ratio of R^2 values for the Gamma and log-Gaussian models is plotted as a function of preferred speed. The Gamma model tends to be superior to the log-Gaussian model for neurons that prefer slow speeds. deg/sec, Degrees per second.

physically, we computed speed discrimination thresholds for the MT population. Because we did not sample speed finely enough to compute neuronal sensitivity directly using receiver operating characteristic analysis (Britten et al., 1992), we instead estimated the sensitivity of each neuron (for a large range of pedestal speeds) from the derivative of the best fit to the tuning curve and a linear fit to the relationship between response variance and mean response [see studies by Yang and Maunsell (2004) and Purushothaman and Bradley (2005) for similar approaches].

Figure 9 illustrates the steps of this procedure for an example neuron. Figure 9A shows the raw speed-tuning data (filled circles), the best-fitting Gamma function [$G(s)$, solid line], and the absolute value of the derivative of this fit [$|G'(s)|$, dashed line]. $|G'(s)|$ gives us a quantitative estimate of the steepness of the tuning curve at each speed. Figure 9B shows the relationship between response variance and mean response for the same neuron (one datum per tested speed). From the best linear fit to these data (in log-log coordinates), we could estimate the variance, σ^2 , of the response of the neuron at any point along the tuning function. For any particular reference speed, s_{ref} , the ratio of $|G'(s_{\text{ref}})|/\sigma(s_{\text{ref}})$ gives an estimate of the ability of this neuron to discriminate small differences in speed.

After fitting the data from each MT neuron as illustrated in Figure 9, we can then estimate the speed discrimination thresholds that would be supported by our population of neurons. Theoretical studies (Seung and Sompolinsky, 1993; Pouget et al., 1998) have shown that, for any unbiased estimator based on a population of neurons, the discriminability (d') of two closely spaced stimuli (s_{ref} and $s_{\text{ref}} + \Delta s$) has an upper bound given by the following:

$$d'(s_{\text{ref}}) = \Delta s \sqrt{I_F(s_{\text{ref}})}, \quad (6)$$

where $I_F(s_{\text{ref}})$ denotes the Fisher information at s_{ref} given by the following:

$$I_F(s_{\text{ref}}) = \sum_{i=1}^N \frac{G_i'(s_{\text{ref}})^2}{\sigma_i(s_{\text{ref}})^2}. \quad (7)$$

In this formulation, N denotes the number of neurons in the population, $G_i'(s_{\text{ref}})$ denotes the derivative of the tuning func-

tion for the i^{th} neuron at s_{ref} , and $\sigma_i(s_{\text{ref}})$ is the SD of the response of the i^{th} neuron at s_{ref} . Note that neurons contribute to the Fisher information and hence d' , in proportion to the magnitude of the derivative of the tuning curve at s_{ref} . This relationship formalizes the notion that fine discrimination depends most heavily on neurons with tuning curves that are steepest around the reference direction, an idea that has recently received experimental support (Purushothaman and Bradley, 2005).

If we assume that speed discrimination is limited by MT neurons, then the predicted threshold for speed discrimination (corresponding to $d' = 1$) is simply given by the reciprocal of $\sqrt{I_F(s_{\text{ref}})}$. We thus computed I_F for a wide range of pedestal speeds (s_{ref}), using the data from all of the neurons in our sample. This metric assumes that all neurons in the population

have independent noise, and thus d' increases with the square root of the number of neurons in the pool. Previous work has shown that this assumption is invalid; specifically, nearby MT neurons typically show weak correlated noise, with correlation coefficients of ~ 0.2 (Zohary et al., 1994). As a result, we may expect that our estimate of population sensitivity will be too high. However, because our main interest is in how population sensitivity varies with s_{ref} , this does not represent a serious problem. Assuming that correlated noise among neurons does not vary strongly with speed preference, noise correlations would only be expected to change the magnitude of neural sensitivity, not how it varies with s_{ref} .

Figure 10A shows the predicted speed discrimination threshold as a function of pedestal speed. Note that the curve has an initial steep rise, followed by an approximately linear increase with pedestal speed. These data are replotted as Weber fractions in Figure 10B (solid line), and a couple of points about this curve are worth noting. First, note that the predicted Weber fraction drops rapidly with speeds up to $\sim 5^\circ/\text{s}$, after which the Weber fraction remains approximately constant with pedestal speed. Thus, the MT prediction obeys Weber's law for speeds above $\sim 5^\circ/\text{s}$. Second, note that the minimum predicted Weber fraction is ~ 0.01 , which is approximately fivefold lower than those exhibited by human observers (McKee and Nakayama, 1984; Orban et al., 1984; De Bruyn and Orban, 1988). This suggests that a moderate-sized population of MT neurons has sufficient sensitivity to account for behavioral performance (Liu and Newsome, 2005). However, there are a variety of factors that complicate this comparison of absolute sensitivity, so it should be interpreted with caution (see Discussion).

The symbols in Figure 10B (values on the right y-axis) show psychophysical speed discrimination data from the studies of McKee and Nakayama (1984) (filled circles) and De Bruyn and Orban (1988) (unfilled squares). Although the absolute values of the Weber fractions are approximately fivefold larger in the psychophysical data, the shape of the curve is nearly identical to our prediction from the MT population (correlation coefficient, $r = 0.97$; $p \ll 0.001$). This close correspondence supports the notion that speed discrimination behavior is limited by the nature of the speed representation in area MT.

Sources of deviation from Weber's law in the MT population prediction

The solid line in Figure 10B was derived from Gamma fits to MT speed-tuning curves, because the Gamma function provided the most accurate description of the data. Careful inspection of this curve shows that Weber fractions start to increase substantially as the pedestal speed falls below $\sim 10^\circ/\text{s}$ (which is also the case for the human psychophysics). We have described several modest, but significant, departures of MT responses from the idealized logarithmic coding scheme of Figure 1A, but it is difficult to appreciate which factors contribute most to the deviations from Weber's law seen at slow speeds. To address this issue, we used the results from other model fits to make additional predictions of Weber fractions from the MT population data.

The thick solid line in Figure 11 again shows the MT prediction obtained from the Gamma fits. For comparison, the dashed line in Figure 11 shows the prediction obtained from fitting MT data with the log-Gaussian model (all parameters free). Thus, differences between the thick solid and dashed lines reflect deviations in the shape of MT-tuning curves from log-Gaussian. The dashed line is a bit flatter than the thick solid line, with a less rapid increase in Weber fractions as pedestal speed drops below $\sim 10^\circ/\text{s}$. Thus, the small but systematic (Fig. 7B) departure of MT speed-tuning curves from log-Gaussian does contribute to deviations from Weber's law at slow speeds.

Next, to assess the impact of deviations from scale invariance, we computed a population prediction from fits of the log-Gaussian model with s_0 and σ fixed to the median values across the population (as in Fig. 5). The thin solid line in Figure 11 shows that fixing the values of s_0 and σ causes clear flattening of the Weber fraction curve relative to the free log-Gaussian model (red line). We also computed a population prediction after fixing the value of s_0 to 0.001, which produces a set of tuning curves that are truly scale invariant over the relevant range of speeds (Fig. 11B, dot-dashed line). This dot-dashed line is virtually flat down to pedestal speeds of $\sim 1^\circ/\text{s}$, indicating that deviations from scale invariance in the MT code are the major contributor to departures from Weber's law at slow speeds. This observation also indicates that mild nonuniformities in the distribution of MT speed preferences (Fig. 8B) have little effect, because the distribution of log speed preferences was very similar for each of the model fits used (ANOVA; $p = 0.19$). Together, these computations show that the exact shape of the Weber fraction curve for MT neurons is dictated mainly by deviations from scale invariance and departures from log-Gaussian tuning-curve shape. Thus, although we emphasized many similarities between the logarithmic coding scheme and the representation of speed in MT, it is the deviations from this idealized logarithmic scheme that allow the MT predictions to capture the departures from Weber's law that are seen in human psychophysics at slow speeds.

Discussion

In human psychophysics, speed discrimination thresholds scale linearly with pedestal speed over approximately a log unit of

Figure 8. Population summary of speed preferences and response variability. **A**, The distribution of preferred speeds is shown as a histogram with linearly spaced speed bins. Note that the distribution is heavily biased toward slow speeds. **B**, The distribution of preferred speeds, replotted as a histogram with octavespaced bins. In this representation, the distribution is closer to uniform. Note that all preferred speeds below $2^\circ/\text{s}$ have been lumped into the lowest bin for this figure. **C**, The variance/mean ratio for each MT neuron is plotted as a function of its preferred speed. See Results for details. deg/sec, Degrees per second.

Figure 9. Illustration of the procedure for estimating discriminability for a single MT neuron. **A**, The speed-tuning curve of a typical MT neuron (filled symbols) is shown in the same format as Figure 3A. The solid line is the best-fitting Gamma function. The dashed line shows the absolute value of the derivative of the Gamma fit. Note that the units are spikes/degrees, because the response difference between each pair of points (in spikes/s) is divided by the speed difference (in degrees/second). **B**, Response variance is plotted as a function of mean response, on log-log coordinates, for the same MT neuron (filled symbols). Each datum corresponds to one tested speed (plus one datum for spontaneous activity). The solid line is the best linear fit to the data. deg/sec, Degrees per second; spikes/deg, spikes per degree; spikes/sec, spikes per second.

speeds from 5 to $60^\circ/\text{s}$ (McKee and Nakayama, 1984; Orban et al., 1984; De Bruyn and Orban, 1988). Thus, like many other perceptual discriminations, speed discrimination follows Weber's law over a substantial range of values. How should a neuronal representation of speed information be organized to account for this aspect of performance? We have described a simple logarithmic coding scheme (Fig. 1A) that can account for constant Weber fractions. In this scheme, the speed-tuning curves of single neurons take a Gaussian form in log speed, and the tuning curves of the population form a scale invariant set. In addition, the speed preferences of the neurons are distributed uniformly in log speed, and the variability of neuronal responses is independent of speed preference. If a population code in the brain obeys these basic constraints, then discrimination performance should follow Weber's law. Although we are not aware of any other studies that have directly tested the predictions of the logarithmic coding scheme, it is worth noting that logarithmic speed coding has been assumed in some previous studies of MT (Churchland and Lisberger, 2001; Priebe and Lisberger, 2004).

By analyzing speed-tuning curves from a large population of MT neurons recorded as part of a previous study (DeAngelis and Uka, 2003), we have shown that the MT population approximately obeys the constraints outlined above. As a result, the population prediction of speed discrimination thresholds obeys Weber's law for speeds larger than $\sim 5^\circ/\text{s}$. Below $5^\circ/\text{s}$, the predicted Weber fractions rise with decreasing speed resulting from mod-

Figure 10. Comparison of speed discrimination performance for the MT population with human speed discrimination data. **A**, Estimated speed discrimination threshold for the MT population is plotted as a function of pedestal speed. Note that threshold values increase approximately linearly with pedestal speed, with some bending of the curve at slow speeds. **B**, The solid line shows the data from **A**, expressed as Weber fractions (left y-axis). Filled symbols (right y-axis) show Weber fractions for human speed discrimination from the study of McKee and Nakayama (1984). Open squares show analogous human data from the study of DeBruyn and Orban (1988). Note the excellent agreement between the shapes of the MT population curve and the two human data sets. deg/sec, Degrees per second.

Figure 11. Exploration of sources of deviation from Weber's law in the MT population prediction. As in Figure 10, the thick solid line denotes the MT prediction based on Gamma fits, and the symbols show data from human psychophysical studies. The dashed line shows the MT prediction based on fits of the log-Gaussian model with all five parameters free to vary for each MT neuron. The thin solid line shows the MT prediction from fits of the log Gaussian model with shape parameters fixed to the median values across the MT population ($s_0 = 0.33$; $\sigma = 1.16$). The dot-dashed line shows the MT prediction from log-Gaussian fits having $s_0 = 0.001$ and $\sigma = 1.16$. These additional predictions show that deviations from scale-invariance and log-Gaussian tuning shape are the main factors causing a rise in Weber fractions for pedestal speeds below $\sim 10^\circ/\text{s}$ (black line). deg/sec, Degrees per second.

est, but significant, deviations of MT coding from the logarithmic scheme. Interestingly, this departure from Weber's law at slow speeds matches almost exactly with that seen in human psychophysical data (Fig. 10B), consistent with the notion that the speed representation in area MT limits psychophysical performance. The psychophysical data also show that Weber fractions for speed discrimination rise markedly at pedestal speeds exceeding $\sim 50^\circ/\text{s}$. Because, for technical reasons, we could not measure the speed tuning of MT neurons at higher speeds, we cannot say whether the MT population activity would account for this aspect of behavior.

It must also be acknowledged that Figure 10B is a comparison of monkey physiology with human psychophysics, and it is possible that speed discrimination behavior in the monkey might be somewhat different. We are not aware of any comparable psycho-

physical data from monkeys that include a wide range of pedestal speeds. However, given that monkey and human performance is so similar in many low-level psychophysical tasks (De Valois et al., 1974a,b), we expect that monkey psychophysics will take the same form as the data in Figure 10B.

Absolute sensitivity

We used a mathematical description of the performance of an optimal estimator (Seung and Sompolinsky, 1993; Pouget et al., 1998) to predict speed discrimination performance from our population of MT neurons. The predicted Weber fractions are several-fold lower (better sensitivity) than is observed in human psychophysics (Fig. 10B). Although this suggests that the activity of a reasonably sized population of MT neurons could

account for speed discrimination, there are several reasons why the comparison of absolute sensitivities in Figure 10B must be taken with considerable caution (Britten et al., 1992; Shadlen et al., 1996; Uka and DeAngelis, 2003). First, the MT prediction assumes an optimal estimator of neural activity, and decision circuits in the monkey's brain may simply not extract information optimally. Second, the MT prediction assumes that noise among neurons is independent, whereas physiological studies have shown that nearby MT neurons share correlated noise (Zohary et al., 1994; Bair et al., 2001; Purushothaman and Bradley, 2005). Correlated noise may or may not reduce the sensitivity of the neural population depending on how speed signals are extracted from the neurons (Abbott and Dayan, 1999; Romo et al., 2003). Moreover, if correlated noise depends strongly on speed preference, this could change the shape of the predicted discrimination function. Third, the MT predictions were made from responses to stimuli presented for 1.5 s, whereas the human psychophysical data were measured using a stimulus duration of 200 ms (McKee and Nakayama, 1984; De Bruyn and Orban, 1988). This duration difference would be expected to account for approximately a factor of two superiority of neuronal thresholds over psychophysical thresholds (Uka and DeAngelis, 2003). Fourth, our MT prediction used a population of 501 neurons, each of which was stimulated at its preferred direction and disparity. We do not know the size of the pool of neurons that contributes to speed discrimination nor how broad the pooling is across neurons that are not optimally stimulated. These factors can have major effects on the predicted sensitivity (Shadlen et al., 1996). Finally, the human thresholds were computed using a criterion d' of 0.675, whereas our MT predictions correspond to $d' = 1$. Equating these criteria would make neurons even more sensitive relative to behavior.

Considering all of these factors, it is quite difficult to make direct comparisons of absolute neural and psychophysical sensitivity. The fact that MT predictions are several-fold lower than human psychophysics suggests that MT neurons could account for the behavior. However, we place more emphasis on the fact that the shape of the Weber fraction curve for the MT neurons matches closely that of the psychophysics (Fig. 10B).

Efficiency of logarithmic coding

It should be noted that the neuronal representation of speed is not required to follow the logarithmic coding scheme to predict near-constant Weber fractions. For example, the tuning curves of the population could depart dramatically from scale invariance, and this departure could be compensated by alterations in the distribution of speed preferences and/or the variability of neurons as a function of preferred speed. Although many such combinations could produce a similar result to that in Figure 10*B*, it is interesting that MT approximately follows the simple scheme that we have outlined. A likely explanation for this finding is that the logarithmic coding scheme is the most efficient way to achieve a trade-off between good performance and near-constant Weber fractions.

To address this possibility further, we performed a series of simulations in which a population of 10 idealized neurons (similar to those in Fig. 1) was used to code speed. A logarithmic coding scheme (Fig. 1*A*) was compared with a linear coding scheme (Fig. 1*C*). In each case, the speed preference and SD of each unit was a free parameter in the simulations, yielding 20 free parameters for each coding scheme. Using the methodology described by Equations 6 and 7, we computed the Weber fraction as a function of pedestal speed for each combination of free parameters. We adjusted the parameters of each coding scheme to minimize both the mean and the SD of the Weber fraction across pedestal speeds (i.e., we minimized the mean + SD). Thus, the goal was to achieve a good compromise between a low Weber fraction and a constant Weber fraction. We found that the logarithmic coding scheme substantially outperformed the linear scheme in this optimization problem (data not shown). In fact, the logarithmic scheme with a common tuning width for all 10 units (11 free parameters) also outperformed the linear scheme in which each unit had an independent tuning width (20 free parameters). These simulation results reinforce the notion that the logarithmic coding scheme of Figure 1*A* is highly efficient.

Sensitivity to slow speeds

Because the majority of speed-tuning curves in MT have their steepest slopes at very slow speeds (Fig. 9*A*), the MT population is most sensitive when discriminating among speeds close to zero (Fig. 10*A*). In fact, the modest departure of MT speed-tuning curves from the log-Gaussian shape (Fig. 7*B*) generally serves to increase sensitivity to very slow speeds. What might be the functional utility of this high sensitivity to slow speeds? Velocity signals from area MT are thought to be critical for driving eye movements (smooth pursuit and catch-up saccades) that we use to track targets of interest (Dursteler et al., 1987; Komatsu and Wurtz, 1988, 1989; Newsome et al., 1988; Groh et al., 1997; Lisberger and Movshon, 1999; Born et al., 2000; Priebe et al., 2001). During smooth pursuit, the goal is to minimize the difference between target velocity and eye velocity (i.e., retinal slip). To adjust rapidly to changes in target velocity, the system should be highly sensitive to small deviations in retinal slip near zero. We suggest that the speed tuning of MT neurons is well adapted to this purpose.

In conclusion, we have shown that a logarithmic, approximately scale-invariant representation of speed in area MT can explain the psychophysically observed dependence of discrimination thresholds on pedestal speed. These findings provide new insight into how the tuning curves of a population of neurons are

organized to support perceptual performance. Recently, it has been reported that neurons in macaque prefrontal cortex represent numerosity using a logarithmic code (Nieder and Miller, 2003). Together, these findings suggest that logarithmic coding may be a general strategy for representing continuous analog variables in the brain.

Appendix

This appendix provides a mathematical description of the conditions that are sufficient for speed discrimination to obey the Weber–Fechner scaling law. Because the discriminability $d'(s)$ is proportional to $\Delta s \sqrt{I_F(s)}$ (Eq. 6), the Weber–Fechner law, $d'(s) \propto \Delta s/s$, will result when the Fisher information, $I_F(s)$, is proportional to $1/s^2$. The Fisher information is given by the following:

$$I_F(s) = \sum_{i=1}^N \frac{G_i'(s)^2}{\sigma_i(s)^2}, \quad (\text{A1})$$

where $G_i(s)$ is the speed-tuning function and $\sigma_i(s)$ is the SD of response for the i^{th} neuron in the population (both functions of the reference speed around which discrimination is performed).

As shown in our study, speed-tuning curves for MT neurons can be fitted with a log Gaussian function (Eq. 2). When the speed of motion is substantially greater than s_0 , the log Gaussian can be approximated as follows:

$$G_i(s) = R_{0i} + A_i \exp \left[-\frac{\log(s/s_i)^2}{2\sigma^2} \right] = R_{0i} + A_i G_0(s/s_i), \quad (\text{A2})$$

where R_{0i} is a DC offset, and A_i is a gain factor. This expression describes a family of tuning curves that are all scaled copies of a common log Gaussian, $G_0()$, where the scaling factor is the inverse of the preferred speed of the neurons, $1/s_i$. The derivative of the tuning curves is given by the following:

$$\frac{dG_i(s)}{ds} = \frac{A_i}{s_i} G_0'(s/s_i), \quad (\text{A3})$$

resulting in the Fisher information given by the following:

$$I_F(s) = \sum_{i=1}^N \left[\frac{A_i}{\sigma_i(s)} \right]^2 \left[\frac{G_0'(s/s_i)}{s_i} \right]^2. \quad (\text{A4})$$

The first condition we assume is that the ratio of the gain A_i to noise $\sigma_i(s)$ is, on average, independent of s and s_i , so the term $(A_i/\sigma_i)^2$ can be replaced by a constant that is approximately the average signal-to-noise ratio of the neurons. The remaining terms in the sum can be rewritten as follows:

$$I_F(s) \propto 1/s^2 \sum_{i=1}^N (s/s_i)^2 [G_0'(s/s_i)]^2, \quad (\text{A5})$$

which leads to the Weber–Fechner law if the density of the preferred speeds, s_i , is proportional to ds/s_i , or equivalently, the distribution of the preferred log speeds, $d\log(s_i)$, is a constant. The expression on the right side can be rewritten as follows:

$$\sum_{i=1}^N (s/s_i)^2 [G'_0(s/s_i)]^2 ds/s_i \approx \int_0^\infty \xi^2 [G'_0(\xi)]^2 d\xi, \quad (\text{A6})$$

where $\xi = s/s_i$ and the term on the right integrates to a constant. This leaves $I_F(s)$ proportional to $1/s^2$.

It should be noted that the above derivation does not require the common underlying tuning function, $G_0()$, to be log-Gaussian (as assumed in the model of Fig. 1A). Our numerical simulations (see Discussion) suggest that the code is most efficient if $G_0()$ is log-Gaussian, but we have not found proof that this is the optimal shape. However, we have demonstrated three basic conditions that are sufficient for speed discrimination to obey the Weber–Fechner law: (1) the tuning curves should be scaled copies of one another (a scale-invariant set); (2) the distribution of the speed preferences of the neurons should be uniform on a log scale; and (3) the relative signal-to-noise ratio of the neurons $(A_i/\sigma_i)^2$ should be uncorrelated with the preferred speeds. These three conditions correspond to the last three features of the logarithmic coding scheme (Fig. 1A) described in our study. The population of MT cells described in this study approximately satisfies all three of these conditions.

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