The spatial profile of macaque MT neurons is consistent with Gaussian sampling of logarithmically coordinated visual representation

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Running head: Log-Gaussian receptive fields of MT neurons

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ABSTRACT

Neurons in extrastriate visual areas have large receptive fields (RFs) compared with those in primary visual cortex (V1), suggesting extensive spatial integration. To examine the spatial integration of neurons in area MT, we modeled MT neurons RFs based on a symmetrical (Gaussian) integration of V1 outputs and tested the model using single-unit recording in two fixating macaque monkeys. Because visual representation in V1 is logarithmically compressed along eccentricity, the resulting RF model is log-Gaussian along the radial axis in polar coordinates. To test the log-Gaussian model, the RF of each neuron was mapped on a 5 × 5 grid using a small patch of random dots drifting at the preferred velocity of the neuron. The majority of MT neurons had RFs with a steeper slope near the fovea and a shallower slope away from the fovea. Among various 2-dimensional (2-D) Gaussian models fitted to the RFs, the log-Gaussian model provided the best description. The fitted parameters revealed that the range of sampling by MT neurons has no systematic relationship with eccentricities, consistent with a recent study for V4 neurons. Our results suggest that MT neurons integrate inputs from constant-sized patches of V1 cortex.
INTRODUCTION

The primate visual system is comprised of hierarchically organized visual areas (Felleman and Van Essen 1991). The primary visual cortex (V1) detects the stimulus energy within particular spatiotemporal frequency bands in small visual fields (Hubel and Wiesel 1962; De Valois et al. 1982; Foster et al. 1985), whereas extrastriate areas perform elaborate processing on visual information transmitted from V1. As a consequence, neurons in extrastriate areas exhibit selectivity for higher-level stimulus features and have large receptive fields (RFs) compared with those in V1 (see Orban 2008 for a recent review). One of this cortical hierarchy proceeds along the dorsal visual pathway from V1 to the posterior parietal cortex via the middle temporal visual area (MT).

The RFs of MT neurons are larger than those of V1 neurons by a factor of 10 (Albright and Desimone 1987), suggesting substantial spatial integration from V1 to MT. However, the fundamental issue of the manner by which individual MT neurons integrate V1 inputs has not been resolved. In this study, we addressed this issue by modeling the RF of MT neurons based on the spatial integration of V1 outputs. Our model takes advantage of the known topography of 2-D visual representation in V1 (Tootell et al. 1982; Van Essen et al. 1984; Horton and Hocking 1996; Adams and Horton 2003; see Fig. 1A). The logarithmically compressed representation along eccentricity in V1 suggests that MT neurons RFs should be modeled as the logarithm of a Gaussian function on the radial axis using polar coordinates. We report here that the RF profiles of MT neurons are asymmetric, with the peak shifted toward the fovea within the RFs; this asymmetry is readily accounted for by our log-Gaussian RF model. We also used the 3-D surface model of area V1 to examine whether the choice of a 2-D or 3-D model has a significant impact on the results. The present results are in line with a recent study examining RFs of V4.
neurons (Motter 2009), and confirm a general principle for transmission of information between cortical areas.

METHODS

The general experimental procedures for single-unit recording from area MT of awake monkeys have been described in detail previously (Uka and DeAngelis 2003). Here, we briefly summarize the procedures with an emphasis on aspects relevant to the present study. All animal care, training, and experimental procedures were in accordance with the National Institutes of Health guidelines and were approved by the Juntendo University Animal Care and Use Committee.

Subjects and surgery

Experiments were conducted using two Japanese macaque monkeys (*Macaca fuscata*), one female (monkey P) and one male (monkey K), weighing 6 and 8 kg, respectively. For each monkey, one hemisphere was used for electrophysiological experiments (left for monkey P and right for monkey K). A post for head restraint and a recording chamber were chronically implanted in each monkey. To monitor eye movements, we implanted scleral search coils into both eyes for monkey P and one eye for monkey K (Judge et al. 1980). The recording chamber was mounted over the occipital cortex ~17 mm lateral and 14 mm dorsal to the occipital ridge at an angle of 25° above the horizontal so that area MT was accessed by passing through the striate cortex and extrastriate visual areas in the lunate sulcus.

Task and visual stimuli

We controlled the behavioral task and data acquisition using a commercial software
package (TEMPO, Reflective Computing, St. Louis, MO). The monkeys were seated and head-restrained in a primate chair. A DLP projector (Mirage S+2K, Christie Digital Systems, Ontario, Canada) back-projected a visual stimulus on a tangent screen positioned 57 cm in front of the monkeys’ eyes. The screen subtended a visual angle of 122° × 91°. Stimuli were presented dichoptically by means of a pair of ferro-electric liquid crystal shutters (DisplayTech, Longmont, CO) that were mounted just in front of the monkeys’ eyes. Stereo half-images for the left and right eyes were presented alternately at a frame rate of 100 Hz (i.e., 50-Hz refresh for each eye) and were synchronized with the vertical refresh of the video input. The monkeys viewed random-dot stimuli while keeping fixation on a yellow dot (0.15°) on the screen. The monkeys received a drop of water as a reward when their conjugate eye position remained within a 2.0° × 2.0° electronic window around the fixation point during stimulus presentation (500 ms). If the monkeys broke fixation during the trial, the trial was terminated, the data were discarded, and the monkeys were not rewarded.

Random-dot stimuli were presented using an OpenGL accelerator board with quad-buffer stereo support (Quadro FX 1400, NVIDIA, Santa Clara, CA). Each random-dot stereogram (RDS) was presented within a circular aperture. Dot density was 64 dots per square degree per second, with each dot subtending ~0.1°. The starting position of each dot was newly randomized for each trial. The RDS consisted of red dots (5.3 cd/m²) presented on a black background (0.10 cd/m²). Precise binocular disparities and smooth motion were achieved by plotting dots with sub-pixel resolution using anti-aliasing provided by the OpenGL board.

**Electrophysiological recordings**

We used a tungsten microelectrode (FHC Inc, Bowdoin, ME) with impedance values
between 0.5 and 2.0 MΩ (at 1 kHz) for recording the extracellular activity of single neurons. The electrode was advanced through the cortex through a transdural guide tube, using a pulse motor micromanipulator (MO-951, Narishige, Tokyo) mounted on the recording chamber. Raw signals from the electrode were amplified and bandpass filtered (200–10000 Hz) with conventional electronic equipment (Bak Electronics, Mount Airy, MD), and we isolated single neurons using a voltage-time window discriminator (Bak Electronics). Times of action potential and trial event occurrence were stored to disk with 1-ms resolution. Eye position was monitored by using a magnetic search coil system (Sankeikizai, Tokyo) and stored to disk at a rate of 250 Hz.

Area MT was identified based on our extensive experience in interpreting the pattern of gray matter and white matter encountered during electrode penetration and on the physiological response properties (direction, speed, horizontal disparity tuning, receptive field location, and size) of both single neurons and multiunit clusters. All data included in this paper were derived from recordings that were confidently assigned to area MT.

**Experimental protocols**

After isolating a single MT neuron, we qualitatively explored RF size and location, as well as the tuning properties (direction, speed, and horizontal disparity) of the neuron using a small circular patch of drifting random dots. Next, we conducted a set of quantitative preliminary tests to measure speed tuning, horizontal disparity tuning, RF size and location, size tuning (area summation), and direction tuning of each MT neuron. Each of these measurements was performed in a separate block of randomly interleaved trials, with each unique stimulus presented at least three times. During these tests, a tuning curve or RF map was constructed.
online, and the preferred stimulus parameter was used in subsequent tests. First, speed tuning was measured by presenting dots that drifted at 0, 1, 2, 4, 8, 16, 32, and 64°/sec. Horizontal disparity tuning was then measured at the preferred speed by presenting dot patterns whose horizontal disparity varied from –1.6° to 1.6° in steps of 0.4°. Next, we mapped the RF by presenting a small (~0.25 × approximate RF diameter) patch of random dots drifting at the preferred speed and horizontal disparity at each location on a 4 × 4 grid that covered the entire RF. A 2-dimensional (2-D) Gaussian function with an identical radius along two cardinal axes (Circle model; see Results) was fit to this RF map. This test was designed to obtain quantitative estimates of the RF center and radius (SD of the fitted Circle model), which were used for detailed RF mapping (see below). After determining the RF center, we assessed size tuning by presenting dots within circular apertures at the RF center. We presented aperture sizes of 1, 2, 4, 8, 16, 32, and 64° in diameter. Subsequently, direction tuning was measured by presenting eight motion directions, 45° apart, with all other parameters optimized.

**Detailed receptive field mapping procedures**

Following the preliminary tests, we obtained a finer-scale RF map. For this detailed mapping, a virtual 5 × 5 grid was positioned at the RF center (Fig. 2A). On each trial, a small circular patch of random dots (probe) drifting at the preferred velocity and the preferred disparity was presented at each grid location. The probe diameter was half of the RF radius, derived as the SD of the 2-D Gaussian (Circle model) fitted to the initial 4 × 4 RF map. The grid spacing was the unit SD from the fitted Circle model. Thus, the full mapping range covered 4.5 × RF radius. We recorded neuronal activity for up to 20 trial repetitions of each unique stimulus condition. Data were discarded if the neuron was lost before three repetitions. The average number of trial repetitions across the range of accepted data sets was 9.4 (4.7 SD). Even when
we restricted data to neurons with trial repetitions $\geq 10$ ($N = 111$), the same results were obtained. Thus, we report below results from the entire population of datasets.

RF mapping during a peripheral discrimination task

To test whether the RF profiles depended on task, we trained one monkey to perform a random-dot motion-direction discrimination task (Britten et al. 1992). In this task, the monkey indicated its decision about the direction of motion by making a saccadic eye movement to one of two choice targets around the fixation point. The monkey was given a liquid reward for correct responses. MT neurons RFs were mapped while the monkey discriminated the direction of random-dot motion presented at a peripheral location outside the RF mapping grid. The random-dot motion being discriminated was set at a distance of three or more times the distance from the fixation point to the RF center. During this task, care was taken so that the mapping grid did not overlap with the random-dot motion being discriminated. The color of the dots being discriminated was set to white ($23 \text{ cd/m}^2$) (the color of the probe dots was red), providing a cue to which dots the monkey had to discriminate. The direction of the random-dot motion was perpendicular to the preferred direction of the neuron under study. Under these conditions, the monkey had to ignore the probe dots. The diameter of the random-dot motion was $20^\circ$, and the motion coherence varied from 3 to 80%. The speed of motion was set to $16^\circ/\text{sec}$, and the horizontal disparity was $0^\circ$. Note that these parameters were irrelevant for the RF mapping. All stimulus conditions were randomly interleaved within a block.

Data analysis

Neuronal responses to each stimulus condition were defined as the mean firing rate across trial repetitions in the time window of visual stimulus duration. Spontaneous firing rate
was calculated from spiking activity during presentation of a blank screen.

We evaluated tuning curves for stimulus speed, horizontal disparity, size, and direction by fitting with analytical functions (see DeAngelis and Uka 2003 for detail). RF maps were fit with various RF models, as described below. We fit the functions to the individual trial responses of the neuron using the constrained minimization tool, fmincon, in MATLAB (Mathworks). As firing rate variance is proportional to the mean firing rate (Dean 1981; Tolhurst et al. 1981), we minimized this dependence by transforming the firing rate into its square root (see Prince et al. 2002). Thus, fitting was achieved by minimizing the sum of squared errors between the square root of the firing rates and the square root of the function. We evaluated the quality of model fit in two ways. First, we calculated the variance in mean firing rates accounted for by the model ($R^2$ values). Second, we performed a $\chi^2$ goodness-of-fit test (DeAngelis and Uka 2003). This test compares residuals around the mean response with residuals around the value of the fitted function.

To determine whether our Polar Log-Gaussian RF model (derived in Results) explained the RF of MT neurons, we also evaluated fits of several other possible RF models. However, comparing the alternative models based solely on $R^2$ values might have given erroneous results because the different models have different mathematical forms and often have a different number of parameters. Therefore, we also used an information theoretic approach and calculated the Akaike Information Criterion (AIC; Akaike 1974). The AIC deals with the problem of overfitting and has now been progressively applied in systems neuroscience (e.g., McCoy and Platt 2005; Seo et al. 2007). The formula of the AIC we used is as follows:
\[
\text{AIC} = 2k + n \left[ \ln \left( \frac{2\pi \text{SSE}}{n} \right) + 1 \right] + n - k - 1
\]

where \( k \) is the number of parameters in the RF model, \( n \) is the number of observations, and the \( \text{SSE} \) is the sum of squared error obtained in the fitting. The model having the lowest AIC value was regarded as the best model.

The confidence interval (CI) was calculated by bootstrap resampling (Efron 1979). A hypothetical dataset was generated by independent random sampling with replacement from the original firing rates at particular stimulus conditions. The RF map was generated from the hypothetical dataset, and this procedure was repeated 1000 times. Derived quantities used in nonparametric analyses (as shown in Figs. 7–9) were calculated for each of 1000 resampled RFs, and the 2.5 and 97.5 percentiles of the 1000 values were used as an estimate of the 95% CI. If the 95% CI of a quantity did not include one (e.g., Fig. 7C), we concluded that the quantity differed significantly from one. Also the 95% CI of fitted parameters of the RF model (as shown in Fig. 10) were obtained by fitting the RF model for each of 1000 resampled RFs.

**RESULTS**

**Modeling RFs of MT neurons**

We first considered how MT neuron RFs are constructed based on sampling visual input from V1. The starting point of our modeling relies on the fact that the visual field is mapped onto V1 in a topographic manner. Here we describe the visual field in polar coordinates, with the radial coordinate denoting the eccentricity \( r \), and the angular coordinate denoting the azimuth \( \phi \), whereas the coordinate in V1 is Cartesian, \((X, Y)\). Imaging studies using 2DG autoradiography and functional magnetic resonance imaging (fMRI) demonstrate that more
In modeling RFs of MT neurons, we assume that an MT neuron receives inputs from V1 with symmetric Gaussian weights such that V1 neurons with the same RF position as the recipient MT neuron provide dense projections (Movshon and Newsome 1996). As shown above, the V1 retinotopic map can be considered separately in horizontal and vertical directions. Accordingly, we consider the sampling ranges on V1 from which a MT neuron receives input separately along horizontal and vertical directions. Let us denote the horizontal sampling range as $\sigma_{\text{sampleX}}$ and the vertical sampling range as $\sigma_{\text{sampleY}}$. Then, the Gaussian sampling weight for horizontal and vertical directions are written as $\exp\{-\frac{(X-X_0)^2}{2\sigma_{\text{sampleX}}^2}\}$ and $\exp\{-\frac{(Y-Y_0)^2}{2\sigma_{\text{sampleY}}^2}\}$, respectively, where $(X_0, Y_0)$ is the center location of the sampling on V1 (Fig. 1, B and D). By substituting the V1 map functions, $X = k \cdot \log(r)$ and $Y = k \phi$, into these sampling functions, we obtain the RF function of a MT neuron along the eccentricity and azimuth directions as
\[ RF(r) = \exp \left\{ -\frac{\left[ \log \left( r / r_0 \right) \right]^2}{2 \left( \sigma_{\text{sample}X} / k \right)^2} \right\}, \]

\[ RF(\phi) = \exp \left\{ -\frac{(\phi - \phi_0)^2}{2 \left( \sigma_{\text{sample}Y} / k \right)^2} \right\}, \]

where \( r_0 = 10^{10/k} \) and \( \phi_0 = Y_0 / k \) indicate the RF center in the visual field in polar coordinates (Fig. 1, C and E). By combining these functions into a single form, we derive the model of the RF profile of MT neurons:

\[ RF(r, \phi) = \exp \left\{ -\frac{\left[ \log \left( r / r_0 \right) \right]^2}{2 \sigma_r^2} \right\} \cdot \exp \left\{ \frac{\cos(\phi - \phi_0)}{2 \sigma_{\phi}^2} \right\} \]

where \( \sigma_r = \sigma_{\text{sample}X} / k \) and \( \sigma_{\phi} = \sigma_{\text{sample}Y} / k \) control the RF width along the radial axis and the angular axis, respectively. The second term was converted from standard Gaussian to circular Gaussian because azimuth is a circular variable. Note that \( \sigma_r \) and \( \sigma_{\phi} \) are unitless quantities because of the formulation within the exponential functions. We introduce one additional parameter into the model to make a MT neuron have a maximum firing rate to visual stimuli.

Thus, the final expression of the Polar Log-Gaussian model of MT neurons RFs is as follows:

\[ Z_{\text{polar-logGaussian}}(r, \phi) = R_{\text{spont}} + A \cdot \exp \left\{ -\frac{\left[ \log \left( r / r_0 \right) \right]^2}{2 \sigma_r^2} \right\} \cdot \exp \left\{ \frac{\cos(\phi - \phi_0)}{2 \sigma_{\phi}^2} \right\} \] \tag{1}

where \( A \) is the amplitude. Note that the baseline of the RF is fixed at the spontaneous firing rate \( R_{\text{spont}} \) and is not a model parameter. Thus, the number of free parameters of the Polar Log-Gaussian model is five.

To test this model quantitatively, we analyzed the RF profiles of single neurons in area MT while monkeys performed a fixation task.
Neuronal database

We recorded activity from a total of 195 neurons from two monkeys (99 neurons from monkey K and 96 from monkey P). For each neuron, we obtained an RF map with $5 \times 5$ resolution (Fig. 2A) using a small circular patch of random dots drifting at that neuron’s preferred direction, speed, and horizontal disparity. Figure 2B shows the location and the size of the RFs of all recorded neurons. The center position and the radius of the RF were derived from the best fitting 2-D Gaussian function (Circle model) as described below. Eccentricities of RFs of all recorded neurons ranged from 4.2° to 54.8°. We sampled MT neurons with RFs of various azimuths and eccentricities.

Receptive field profiles of MT neurons

A representative data set from one MT neuron is shown in Figure 3. This example neuron responded vigorously to zero-disparity dots (Fig. 3B) drifting rightward and slightly downward (Fig. 3C) at an intermediate speed of ~16°/sec (Fig. 3A). The preliminary RF mapping at $4 \times 4$ resolution revealed that the RF center was (7.1°, 5.8°) with a radius (SD of the fitted Circle model) of 2.7°. From these parameters, we defined the RF mapping range as 12.15° x 12.15° (4.5 SD x 4.5 SD) and the diameter of a probe patch as 1.35° (0.5 SD). The raw RF map obtained with these parameters is shown in Figure 3D. In this plot, mean firing rates at each grid location are represented as colors, as indicated in the color bar.

We examined the spatial profile of the RF of the example neuron shown in Figure 3D and whether it conformed to the Polar Log-Gaussian model. We created the RF surface by interpolating the raw RF map with a 2-D cubic spline surface as shown in Figure 4 (‘Spline’ map). Inspection of the spline RF map in Figure 4 revealed that the circumference of the RF is
circular, but response slopes are not isotropic. Instead, the RF had a steeper slope near the fovea and a shallower slope away from the fovea, as shown by the density of the iso-response contours. Accordingly, the response peak did not occur at the RF center, but was shifted toward the fixation point (the cyan square in Fig. 4) within the circumference of the RF. This suggests that MT neurons RFs are consistent with the Polar Log-Gaussian model.

To quantify this observation, we fit the RF map with the Polar Log-Gaussian model (Eq. 1). To test whether this model provides a concise description of MT neuron RFs, we also fit RF maps with four other models and compared fit quality. First, we fit RFs of MT neurons with the Circle model described as

$$Z_{\text{circle}}(x, y) = R_{\text{spont}} + A \cdot \exp \left( \frac{(x-x_0)^2}{2\sigma_x^2} \right) \cdot \exp \left( -\frac{(y-y_0)^2}{2\sigma_y^2} \right)$$  \hspace{1cm} (2)$$

where $A$ is the amplitude, $(x_0, y_0)$ is the center position of the Gaussian in Cartesian coordinates, and $\sigma$ is the SD. For the Circle model, widths along the two cardinal axes are identical. Again, $R_{\text{spont}}$ is not the model parameter, but a fixed value representing spontaneous firing rate. This model provides the center position and the radius of the RF (Fig. 2B). The number of free parameters of the Circle model is four. Second, we fit RF maps with the Oriented model given as

$$Z_{\text{oriented}}(x, y) = R_{\text{spont}} + A \cdot \exp \left( -\frac{\alpha^2}{2\sigma^2} \right) \cdot \exp \left( -\frac{\beta^2}{2\sigma^2} \right),$$  \hspace{1cm} (3)$$

with

$$\begin{align*}
\alpha &= (x-x_0)\cos(\theta) + (y-y_0)\sin(\theta) \\
\beta &= -(x-x_0)\sin(\theta) + (y-y_0)\cos(\theta)
\end{align*}$$

where $\sigma_{\alpha}$ and $\sigma_{\beta}$ are the SDs along the minor and major axes, and $\theta$ is the rotation angle. Other
parameters are identical to the Circle model. For the Oriented model, the widths can be different, and cardinal axes can have arbitrary angles. This Oriented model has been used in previous studies to describe MT neuron RFs (Raiguel et al. 1995; Britten and Heuer 1999; Womelsdorf et al. 2008). The number of free parameters of the Oriented model is six. Third, we used the Polar Gaussian model of the form

\[ Z_{\text{polar-Gaussian}}(r, \phi) = R_{\text{spont}} + A \cdot \exp \left\{ -\frac{(r-r_0)^2}{2\sigma_r^2} \right\} \cdot \exp \left\{ \frac{\cos(\phi-\phi_0)}{2\sigma_\phi^2} \right\}. \] (4)

This model has the same number of free parameters as the Polar Log-Gaussian model. Note that the width parameter \( \sigma_r' \) has units of degrees (unlike for the Polar Log-Gaussian model). The function along the radial axis is a standard Gaussian, instead of the log-Gaussian used in the Polar Log-Gaussian model. The number of free parameters of the Polar Gaussian model is five. Finally, we also examined the logarithm of Gaussian defined in Cartesian coordinates (the Cartesian Log-Gaussian model). To get around the problem of log transformation of negative values, we constrained the axis of log transformation to be along the line between the fixation point and the Gaussian center, and multiplied absolute log-transformed values by \(-1\) for negative values. An offset parameter is introduced to prevent log transformed values from becoming negative. Let us denote this transformed coordinate as \((x', y')\). The Cartesian Log-Gaussian model is defined in this coordinates as:

\[ Z_{\text{cartesian-logGaussian}}(x', y') = R_{\text{spont}} + A \cdot \exp \left\{ -\frac{\alpha^2}{2\sigma_\alpha^2} \right\} \cdot \exp \left\{ -\frac{\beta^2}{2\sigma_\beta^2} \right\}, \] (5)

with

\[
\begin{align*}
\alpha &= \{x' - r \cos(\theta)\} \cos(\theta) + \{y' - r \sin(\theta)\} \sin(\theta), \\
\beta &= -\{x' - r \cos(\theta)\} \sin(\theta) + \{y' - r \sin(\theta)\} \cos(\theta),
\end{align*}
\]

where \( \sigma_\alpha \) and \( \sigma_\beta \) are the SDs along the minor and major axes, \( r \) is the distance from the fixation point.
point to the Gaussian center on the log-transformed coordinate and $\theta$ is the rotation angle. The number of free parameters of the Cartesian Log-Gaussian model is six.

Figure 4 shows all the Gaussian models fitted to the RF of the example neuron, along with the spline RF map. The display range of the RF map and the fits are enlarged in these plots to include the fixation point (cyan square) for visualizing differences between models defined in Cartesian coordinates and those defined in polar coordinates. Of all the models we examined, the Polar Log-Gaussian model (Eq. 1) provided the best fit to the RF ($R^2 = 0.961$). Comparison of fit quality between different models should clarify factors contributing to the superiority of the Polar Log-Gaussian model. Because the RF had a single peak, the Circle model (Eq. 2), the simplest model we tested, accounted for 88% of response variance ($R^2 = 0.884$). Allowing the model to have different RF widths along the two orthogonal axes and an arbitrary angle provided a marginally better fit for this example neuron ($R^2 = 0.896$, Oriented model (Eq. 3)). Converting the coordinate from Cartesian to polar provided a better description of the RF. The goodness of fit of the Polar Gaussian model (Eq. 4) is satisfactorily high (0.928), yet is still lower than the Polar Log-Gaussian model. This difference is primarily because the RF peak is shifted toward the fovea, which can be explained by simply assuming a sampling with Gaussian weight from the logarithmic map in V1. Applying logarithm transformation of Gaussian in Cartesian coordinates also provided a good description of the RF ($R^2 = 0.935$, Cartesian Log-Gaussian model (Eq. 5)), yet this was also lower than the Polar Log-Gaussian model.

Other representative neurons with RFs that were best described by the Polar Log-Gaussian model are shown in Figure 5. These neurons were selected to demonstrate that MT neurons with RFs of various positions in the visual field all conform to the Polar
Log-Gaussian model.

Results for the entire population of MT neurons are summarized in Figure 6. In all panels, the $R^2$ value for the Polar Log-Gaussian model is plotted against the $R^2$ value for the other model. Figure 6A compares the $R^2$ values for the Circle model and the Polar Log-Gaussian model. The median $R^2$ was 0.873 and 0.913 for the Circle model and Polar Log-Gaussian model, respectively. The vast majority of data points lie above the unity slope diagonal, leading to a highly significant difference in $R^2$ values (Wilcoxon signed-rank test, $p = 1.62 \times 10^{-16}$). The number of neurons that passed a $\chi^2$ goodness-of-fit test ($p > 0.05$) was larger for the Polar Log-Gaussian model (145/195, 74%) than that for the Circle model (126/195, 65%).

Figure 6B compares the quality of fit for the Oriented model and the Polar Log-Gaussian model. The median $R^2$ value for the Oriented model (0.886) was also significantly lower than that for the Polar Log-Gaussian model (0.913) (Wilcoxon signed-rank test, $p = 9.30 \times 10^{-6}$) despite the Oriented model having more parameters than the Polar Log-Gaussian model. About 64% of neurons (124/195) passed a $\chi^2$ goodness-of-fit test for the Oriented model. Thus, although the Oriented model has been widely used in previous studies (Raiguel et al. 1995; Britten and Heuer 1999; Womelsdorf et al. 2008), the Polar Log-Gaussian model provides a better description of MT neuron RFs.

Figure 6C compares $R^2$ values of the Polar Log-Gaussian model and the Polar Gaussian model. As described above, the difference in these two models is the function along the radial axis in polar coordinates: the standard Gaussian in the Polar Gaussian model and the log-Gaussian in the Polar Log-Gaussian model. The median $R^2$ value for the Polar Gaussian...
model (0.908) is sufficiently high. For the majority of MT neurons (115/195), however, the
Polar Log-Gaussian model is superior, as indicated by the significant difference between $R^2$
values (Wilcoxon signed-rank test, $p = 0.004$). The number of neurons that passed a $\chi^2$
goodness-of-fit test for the Polar Gaussian model (141) was slightly less than for the Polar
Log-Gaussian model (145).

There was no significant difference between the $R^2$ values of the Polar Log-Gaussian
model and the Cartesian Log-Gaussian model (Fig. 6D; Wilcoxon-signed rank test, $p = 0.11$),
despite the Cartesian Log-Gaussian model having one more parameter than the Polar
Log-Gaussian model. The number of neurons that passed a $\chi^2$ goodness-of-fit test for the
Cartesian Log-Gaussian model (149) was slightly larger than for the Polar Log-Gaussian model
(145). These comparisons suggest that RFs of MT neurons are better described by a model using
the logarithm transformation than a model without the transformation.

We next compared the quality of model fits using the AIC because comparing models
with different numbers of parameters using $R^2$ values can be potentially difficult. The AIC
handles the problem of overfitting by applying a penalty that increases with increasing numbers
of model parameters. Although the AIC cannot provide statistical testing of alternative models,
it is useful for selecting the best model among several competing models. The numbers of
neurons with the lowest AIC value for the Circle, Oriented, Polar Gaussian, Cartesian
Log-Gaussian, and Polar Log-Gaussian models were 14, 25, 42, 50, and 64, respectively. These
results complement the analysis performed using $R^2$ values and confirm that the RFs of MT
neurons are best described with the Polar Log-Gaussian model.
Nonparametric analysis of the shift of RF peak toward the fovea

The analysis so far relied on fitting a number of models to empirically determined RFs of MT neurons. We performed two additional nonparametric analyses to test the possibility that the above results were dependent on the specific model used. If a MT neuron receives inputs with symmetric weights, the resulting RF should be asymmetric, with the peak shifted toward the fovea and the slope steeper near the fixation point than far from the fixation point (see Fig. 1C). We tested these predictions by first comparing the RF peak position and the RF center position relative to the fixation point and then comparing the slopes of both ends of the RF peak.

If the first prediction holds, the RF peak position should lie between the fixation point and the RF center position. To test this, the peak position of the spline interpolated RF surface was compared with the RF center obtained from the Circle model fit. Figure 7A shows these procedures for the representative MT neuron shown in Figure 3D. The white square and the red dot denote the RF center and RF peak position, respectively. For this particular neuron, the peak position is indeed located between the fixation point (the cyan square) and the RF center. To quantify the degree of peak shift toward the fovea, we first normalized the distance between the fixation point and the RF peak to the distance between the fixation point and the RF center to define a normalized RF peak distance. If the peak is shifted toward the fixation point, then the normalized RF peak distance should be $< 1$. We next calculated the difference in angle between the line connecting the RF center and the fixation point and the line connecting the RF peak and the fixation point. Negative angle differences indicate that the RF peak position is shifted counter-clockwise (CCW) compared to the RF center position relative to the fixation point. If the peak was shifted toward the fixation point, this angle difference should be zero. For the
Results of these analyses across the whole population are summarized in Figure 7, B–D. Figure 7B shows a polar representation of the normalized RF peak distances and angle differences for the entire population. The median values are denoted by the red dot. The median normalized RF peak (0.876; filled triangle in Fig. 7C) was significantly smaller than 1 (sign test, $p = 1.36 \times 10^{-27}$). More than two-thirds of the neurons (69%, 135/195) had normalized RF peak distances significantly different from 1 (bootstrap resampling, $p < 0.05$; filled bars in Fig. 7C) and 129 out of 135 neurons had values < 1. For the angle difference, the distribution was centered at zero, and the median (0.423°; filled triangle in Fig. 7D) was not significantly different from zero (sign test, $p = 0.39$). Individually, 44% of neurons (86/195) had angle differences significantly different from zero (bootstrap resampling, $p < 0.05$; filled bars in Fig. 7D). Of these, 40 neurons had angle differences < 0 and 46 neurons had values > 0.

We next examined the second prediction that the RF slope near the fixation point was steeper than that on the other side of the peak. Figure 8, A and B, illustrates the analysis procedures for the example neuron shown in Figure 7A. We created a 1-D slice of the RF surface through the fixation point and the peak of the RF surface (Fig. 8A) and calculated its first derivative (Fig. 8B). The maximum absolute slope value near the fixation point (upward arrow in Fig. 8B) was compared with that on the far side of the peak (downward arrow in Fig. 8B). Across the population, there was a significant difference between the two maximum absolute slope values (Fig. 8C; Wilcoxon-signed rank test, $p = 7.90 \times 10^{-25}$) and, individually, 115 neurons showed slope values that were significantly different (bootstrap resampling, $p < 0.05$). Of these, 111 neurons exhibited steeper slope near the fixation point than far from the
fixation point. These results complement our parametric analysis and confirm that MT neurons have an asymmetric RF in which the peak is shifted toward the fixation point.

**Eye position has little effect on measured RF maps**

Our monkeys’ fixation was much more precise than imposed with the $2.0^\circ \times 2.0^\circ$ window. Averaged across all experiments, the SDs of horizontal and vertical eye positions across trials were $0.18^\circ$ and $0.19^\circ$, respectively. By comparison, the within trial SDs for horizontal and vertical eye positions were both $0.08^\circ$. Nevertheless, small variability in eye positions within the fixation window may have affected the RF measurement, especially for small RFs, and could pose a significant problem on our results. Specifically, if the monkeys tended to look away from the mapping probe stimulus, and if the deviations were larger for trials with probes of smaller eccentricity, a symmetrical Gaussian RF may appear to be asymmetrical like a log-Gaussian distribution.

To test this possibility, we performed a series of analyses of eye positions or eye drifts within the fixation window. We first examined the dependence of eye position deviation on probe eccentricity. To compensate for calibration errors, we calculated the mean time-averaged eye position (separately for horizontal and vertical directions) across all trials during the stimulus viewing period. For each trial, the eye position deviation was calculated by subtracting the mean eye position from the time-averaged eye position for that trial. This yielded a zero-centered distribution of eye position deviations for horizontal and vertical directions. We then quantified the eye position deviations in the direction of the RF mapping grid by projecting eye position deviation data onto a line connecting the mean eye position and the center of the RF mapping grid. If deviations opposite to the RF mapping grid were larger for trials with
probes of smaller eccentricity, this should result in a positive correlation between eye position
development and probe eccentricity. For the vast majority of data (180/195), however, the
correlation was not significant ($p > 0.05$). Similarly, no correlation was observed for 186/195
datasets even if the probe positions were projected onto the line connecting the fixation point
and the grid center, or when eye position deviations were projected onto the line connecting the
fixation point and the respective probe positions. For eye drift analysis, we first quantified eye
drift as the vector from the initial eye position to the final eye position during the stimulus
viewing period. If eye positions drifted away from the mapping stimulus at smaller probe
eccentricities, we would expect a negative correlation between the magnitude of the eye drift
vector and probe eccentricity. Rather, we found that for the majority of datasets (158/195) the
correlation was not significant ($p > 0.05$). Even if we exclude neurons with significant
correlation, the basic results were reproducible. Comparisons of $R^2$ values yielded a statistically
significant difference between the Polar Log-Gaussian model and the Circle model (Wilcoxon
signed-rank test, $p = 8.69 \times 10^{-17}$), between the Polar Log-Gaussian model and the Oriented
model ($p = 2.97 \times 10^{-7}$), and between the Polar Log-Gaussian model and the Polar Gaussian
model ($p = 1.48 \times 10^{-4}$) but not between the Polar Log-Gaussian model and the Cartesian
Log-Gaussian model ($p = 0.670$). From these analyses, we conclude that small variability in eye
positions had minimal effects on our RF measurements and hence our results.

**Log-Gaussian RF does not change during a peripheral discrimination task**

We mapped RFs for a subset of neurons from monkey P while the monkey performed
a direction discrimination task at a far peripheral location in a separate block of trials as well as
during the fixation task. Figure 9, A and B, shows example datasets for a single experiment. For
this neuron, the initially estimated RF center was $(7.3^\circ, 6.5^\circ)$. We set the position of random-dot
motion such that the monkey had to discriminate at a distance three times farther than that from
the fixation point to the RF center, (21.9°, 19.5°). The monkey discriminated between 90° CW
and 90° CCW to the preferred direction of this neuron. During the presentation of random-dot
motion, the probe was also presented using the exact same grid as the RF mapping performed
during the fixation task. We obtained data sets from 22 neurons for which RF mapping during
the discrimination task was completed.

Figure 9A shows the psychometric function for an example experiment in which the
proportion of 90° CW choices is plotted against the signed motion coherence of the random-dot
motion. A steep slope at weak motion coherences and perfect discrimination performance at the
strongest motion coherences (80% and –80%) suggest that the monkey successfully
discriminated motion direction at the peripheral location. There was a small, but systematic shift
in mean eye position (0.21°) toward the patch of white random dots during the discrimination
task compared with the fixation task. Across the population, the average shift in mean eye
position was 0.14° (SD 0.13°). Because this shift could potentially affect our RF measurements,
we performed the same analysis of eye position variability as in the previous section. No
correlation was found between the eye position deviation and the probe eccentricity for 21 out
of 22 datasets (p > 0.05) during the discrimination task. Thus, despite an overall shift in eye
position, the eye position variability did not confound with RF measurements even during the
discrimination task.

Spline RF maps and associated Polar Log-Gaussian fits obtained during the fixation
and discrimination tasks for this representative MT neuron are shown in Figure 9B. The spline
RF maps and the Polar Log-Gaussian fits obtained during the two tasks are virtually identical,
suggesting that the Polar Log-Gaussian model still provided an adequate description of RFs obtained during the discrimination task. Figure 9C displays the results obtained during the discrimination task in the same manner as Figure 6. The Polar Log-Gaussian model was superior to all other models (Wilcoxon signed-rank test, \( p < 0.005 \)) except the Cartesian Log-Gaussian model (Wilcoxon signed-rank test, \( p = 0.338 \)). The median \( R^2 \) values for the Polar Log-Gaussian fit, the Cartesian Log-Gaussian fit, the Polar Gaussian fit, the Oriented fit, and the Circle fit were 0.930, 0.931, 0.906, 0.895, and 0.880, respectively.

We further performed the same nonparametric analysis as in Figure 7 in which the peak shift towards the fovea was quantified. Figure 9, D and E, compares the distributions of the normalized RF peak distances and the angle differences, respectively, between the two tasks for the 22 neurons. For the RF mapped during the discrimination task, the median normalized RF peak (0.898; filled triangle in the bottom histogram in Fig. 9D) was significantly smaller than 1 (sign test, \( p = 1.10 \times 10^{-5} \)). The distribution of the angle difference was centered at zero, and the median (0.30°; filled triangle in the bottom histogram in Fig. 9E) was not significantly different from zero (sign test, \( p = 0.524 \)). These two measures were statistically indistinguishable between the fixation and the discrimination task (Wilcoxon signed-rank test, \( p = 0.465 \) for the normalized RF peak distance, \( p = 0.733 \) for the angle difference). Thus, it seems that our RF measurement was not confounded with task demands (fixation vs. discrimination) and do not strongly depend on precise eye positions.

**Correction of stimulus position**

We used a tangent screen measuring 122 × 91 cm at a viewing distance of 57 cm for stimulus presentation. This makes the stimulus placement at the extreme screen periphery
inappropriate. The actual stimulation point on the retina is the angle difference between gaze
direction and the direction from which rays of light emitted by the stimulus comes. For example,
suppose that the stimulus is presented at the rightmost edge of the tangent screen, \((61^\circ, 0^\circ)\) in
screen coordinates. The actual stimulation point can be calculated as \(57 \times \tan^{-1}(61/57) \approx 46.7^\circ\).

We determined whether this underestimation of peripheral stimulus position affected our results.
For each neuron, the probe positions were transformed from screen coordinates into retinal
coordinates using the trigonometric relationship between the viewing distance and the stimulus
position on the screen. We then fitted all RF models to the RF map defined by the transformed
retinal coordinates.

The Polar Log-Gaussian model provided a better description of the RF using retinal
coordinates than did the Circle model (Wilcoxon signed-rank test, \(p = 3.29 \times 10^{-13}\)) or the
Oriented model (Wilcoxon signed-rank test, \(p = 0.016\)), however, no significant difference was
found between the \(R^2\) values of the Polar Log-Gaussian model and those of the Polar Gaussian
model (median \(R^2\) value = 0.909 and 0.906 for the Polar Log-Gaussian and the Polar Gaussian,
respectively; Wilcoxon signed-rank test, \(p = 0.12\)). The \(R^2\) values of the Cartesian Log-Gaussian
model (median \(R^2\) value = 0.919) were slightly larger than those of the Polar Log-Gaussian
model (Wilcoxon signed-rank test, \(p = 0.006\)). The lack of difference in the \(R^2\) values between
the Polar Log-Gaussian model and the Polar Gaussian model is largely because at large
eccentricities, the mapping grid was distorted such that the outermost point within the grid was
compressed toward the fixation point. Indeed, if we restrict our analysis to neurons with
eccentricities smaller than the median \((N = 97)\), there was a significant difference in \(R^2\) values
between the Polar Log-Gaussian model and the Polar Gaussian model (Wilcoxon signed-rank
test, \(p = 5.27 \times 10^{-4}\)). We also found that the ratio of \(R^2\) values for the Polar Log-Gaussian model
defined in retinal coordinates and those defined in screen coordinates was negatively correlated
with RF eccentricity (Spearman’s rank correlation $r_s = -0.40$, $p = 7.50 \times 10^{-9}$, data not shown),
whereas for the Polar Gaussian model, no such correlation existed (Spearman’s rank correlation
$r_s = -0.05$, $p = 0.46$). This suggests that for MT neurons with large eccentricities our mapping
method could not adequately sample the region where neuronal responses fall off toward the
periphery.

However, the AIC still showed that the Polar Log-Gaussian model and the Cartesian
Log-Gaussian model were the best models for describing the RFs of MT neurons, even defined
in retinal coordinates. The numbers of neurons with the lowest AIC value for the Circle,
Oriented, Polar Gaussian, Cartesian Log-Gaussian and Polar Log-Gaussian models in retinal
coordinates were 11, 40, 36, 56 and 52, respectively. These data provide further evidence that
the Polar Log-Gaussian model and the Cartesian Log-Gaussian model are the most
parsimonious model for describing the RF of MT neurons.

Estimation of sampling range from V1 surface

We next examined the fitted parameters of the Polar Log-Gaussian model to obtain
insights into the manner in which MT neurons integrate signals from V1. Relevant parameters
are the RF width parameter along the radial axis ($\sigma_r$) and along the angular axis ($\sigma_\phi$). Figure 10,
A and B, shows dependency of these RF width parameters on RF eccentricities. No significant
correlation was found between $\sigma_r$ and RF eccentricity (Spearman’s rank correlation $r_s = 0.02$, $p$
= 0.813) or between $\sigma_\phi$ and RF eccentricity (Spearman’s rank correlation $r_s = -0.01$, $p = 0.852$).
The $\sigma_\phi$ was larger than the $\sigma_r$ (median values were 0.30 for $\sigma_\phi$ and 0.20 for $\sigma_r$; Wilcoxon
signed-rank test, $p = 1.71 \times 10^{-30}$, Fig. 10C). The range of integration by MT neurons along the
two orthogonal directions in V1 can be calculated from the $\sigma$ and $\sigma_{\phi}$ of the Polar Log-Gaussian fit, that is, $\sigma_{\text{sampleX}} = k \cdot \sigma$ and $\sigma_{\text{sampleY}} = k \cdot \sigma_{\phi}$. With a scaling parameter $k$ of 8.72 (Polimeni et al. 2006), the sampling range from area V1 along the horizontal direction ($\sigma_{\text{sampleX}}$) and along the vertical direction ($\sigma_{\text{sampleY}}$) have median values of 2.6 mm and 1.7 mm, respectively. However, these values depend on the scaling parameter of the complex logarithmic model, and the exact value of the scaling parameter remains controversial. Thus, although the exact values of sampling range cannot be determined by our study, the relationship between the two sampling ranges should not be affected by the choice of the scaling parameter. These results suggest that there is no systematic relationship between the sampling range of MT neurons and the RF eccentricity and that MT neurons might integrate inputs from V1 cortex with an elliptical 2-D Gaussian weight.

3-D V1 model

So far, we have used the complex logarithmic map of area V1 for modeling the RF of MT neurons. The complex logarithmic map is a transformation of the 3-D surface of a hemisphere in area V1 into a 2-D sheet. Although widely used in the literature, any mapping from 3-D to 2-D space inevitably produces some distortion, and this distortion could affect our results. A recent paper examining the RF of V4 neurons (Motter 2009) used the 3-D surface model for area V1 (Rovamo and Virsu 1984) instead of the flat 2-D map. To examine the degree to which the choice of a particular V1 model impacts the results, we applied the same analysis as Motter (2009) using the curved V1 surface model.

In this analysis, a point in visual space is represented using polar coordinates as $(\theta, w)$ with azimuth $\theta$ and eccentricity $w$. The projection point on the curved V1 surface is represented
using cylindrical coordinates \((r, z, \phi)\), where \(r\) is the distance from the axis of rotation, \(z\) is the distance from the fovea along the axis of rotation, and \(\phi\) is the rotation angle (Fig. 11A). As shown in Rovamo and Virsu (1984), assuming only the local isotropy of the cortical magnification, we can derive the equations that define the 3-D surface of V1:

\[
\begin{align*}
  r &= M(w) \sin w \\
  z &= \sqrt{\int_0^w [M(w)^2 - (dr/dw)^2]^{0.5}} dw \\
  \phi &= \theta
\end{align*}
\]

where \(M(w)\) denotes the linear cortical magnification factor along eccentricity. As in Motter (2009), we used \(M(w)\) as the square root of the areal magnification factor taken from LeVay et al. (1985), that is, \(M(w) = 10(0.8 + w)^4\). The 3-D surface model of V1 was constructed for a full range of azimuths from \(-\pi\) to \(\pi\) radians and for eccentricity up to 85°, and the model is shown in Figure 11B as an orthographic projection. In this figure, the fovea is represented at the leftmost end, and the far periphery is represented at the rightmost edge of the projection.

The RF map of each MT neuron was back-projected onto the 3-D surface of the V1 model using Eq. 6. The red solid lines in Figure 11B denote the back-projected, spline interpolated RF contour of the representative neuron shown in Figure 3. Consistent with V4 neurons (Motter 2009), the asymmetry evident in the RF map in Figure 3D was removed in the back-projected RF contour, and it appears to have a symmetric shape. To quantify this, the back-projected RF contour on V1 surface was fit with a 2-D Gaussian function. The fit was performed such that one of the two cardinal axes of the fitted Gaussian is parallel to the meridian line connecting the center of the back-projected mapping grid and the fovea. The degree of circularity was quantified using the ratio of the radii (short/long) of the fitted Gaussian.
The distribution of the short/long radius ratio across the population is shown in Figure 11C. The average short/long ratio was 0.810 (open triangle in Fig 11C; median 0.818, filled triangle in Fig 11C). However, from this analysis the axis of elongation is unclear. We thus compared the radius of the fitted Gaussian orthogonal to the meridian line and the radius parallel to the meridian. The ratio of radii orthogonal/parallel to the meridian is shown in Figure 11D. The median value of 0.905 (filled triangle in Fig 11D) was significantly smaller than 1 (sign test, \( p = 1.42 \times 10^{-4} \)). These results suggest that the axis of elongation as a whole is parallel to the meridian line, but the degree of elongation is small.

The RF model based on the complex logarithmic map revealed that the sampling area of MT neurons has no systematic relationship with the RF eccentricity (Fig. 10, A and B). We next determined whether this constant but variable sampling is specific to the complex logarithmic map by examining the relationship between the RF eccentricity and the radius (SD) of a ‘Circle’ Gaussian fitted to the back-projected RF contours on the curved V1 surface. The radius ranged from 2 to 6 mm, and the mean value was 4.01 mm (Fig. 11E). These values are comparable to V4 neurons (Motter 2009). No correlation was found between the radius and the eccentricity (Spearman’s rank correlation \( r_s = -0.06, p = 0.41 \); Fig. 11E). Thus, the constant but variable sampling by MT neurons did not result from the specific V1 model. Together with results obtained for V4, it represents a general principle of transmission of information from one visual area to the next.

**DISCUSSION**

In this study, we modeled the RF of MT neurons based on a Gaussian sampling from the V1 surface and tested the model by quantitative MT neuron RF mapping. We found that MT
neurons have asymmetric RFs in which the peak was shifted toward the fovea. This asymmetric RF is well described with the Polar Log-Gaussian model using a log-Gaussian along the radial axis and a circular Gaussian along the angular axis in polar coordinates. Furthermore, the estimated sampling range did not depend on the RF eccentricity.

Although statistically significant, the difference in quality of fits between the Polar Log-Gaussian model and the Polar Gaussian model was small for our sample of MT neurons (Fig. 6C). However, the nonparametric analyses confirmed that the RF peak indeed shifted toward the fovea, consistent with the Polar Log-Gaussian model (Figs. 7 and 8). The difference in quality of fits between the Polar Log-Gaussian model and the Cartesian Log-Gaussian model was not significant. RF mapping with finer resolution should provide more concrete data on which model best describes the RF.

Log-Gaussian representation of RFs

Several studies have examined the 2-D RF profiles of MT neurons (Raiguel et al. 1995; Britten and Heuer 1999; Womelsdorf et al. 2008). These studies used the Oriented model to describe RF profiles because of its flexibility in quantifying single-peak RFs and deriving RF parameters such as center locations or sizes. However, in those studies, no attempt was made to quantify the RF profiles of MT neurons.

In brain areas involved in the control of saccadic eye movements, such as the lateral intraparietal area (LIP) or frontal eye field (FEF), neurons have visual RFs as well as movement fields (MFs) that are sensitive to the amplitude and direction of an impending saccade. Although Gnadt and Breznen (1996) applied various 2-D Gaussian models to quantify the visual RFs of
LIP neurons, they did not find any evidence for the superiority of the Polar Log-Gaussian model. This failure may be attributable to the fact that their mapping grid (3 × 3 or 4 × 4) was not fine enough to accurately quantify visual RFs, as subsequent studies demonstrated asymmetry in RFs and/or MFs for LIP neurons (Platt and Glimcher 1998; Ben Hamed et al. 2001). However, the asymmetric RFs in LIP have not been quantified and examined with RF models. The MFs of FEF neurons have also been shown to be asymmetric, with the peak sensitivity shifted toward small saccade amplitude, and are well described using a Gaussian of the logarithm of saccade amplitude (Bruce and Goldberg 1985). The authors suggest that the log-Gaussian tuning for saccade amplitude could reflect logarithmic visual representation in V1.

A recent study quantified the RFs of neurons in visual area V4, an intermediate processing stage along the ventral visual pathway (Motter 2009). V4 neurons also have asymmetric RFs in which the peak is shifted toward the fovea within a circular RF. This author estimated the V1 area from which individual V4 neurons receive inputs by back-projecting the RF contours onto the surface of the 3-D model of V1, as proposed by Rovamo and Virsu (1984). With this V1 model, the estimated sampling region by V4 neurons is circular and has a constant area independent of the eccentricity. Our results are consistent with those observed with V4 neurons and suggest the same principle of projection between cortical areas holds for both the ventral and the dorsal visual pathways.

Previous studies have suggested that spatial attention shifts RF peaks for MT neurons toward an attended location (Womelsdorf et al. 2006, 2008). In our experiment using the direction discrimination task the monkey might have directed its attention toward the peripheral white patch, because the monkey was able to predict neither motion direction nor coherence of
an upcoming dot motion. If so, for RF maps obtained during direction discrimination at the far
periphery, the peak might shift toward the peripheral white patch compared with RF maps
obtained during the fixation task. We failed to observe such shifts in this experiment. Rather, RF
maps obtained during the discrimination task still conformed to the Polar Log-Gaussian model
(Fig. 9C) and the peak shifts were comparable during fixation and discrimination (Fig. 9D).
These results are reasonably consistent with previous studies. Womelsdorf et al. (2006) reported
a significant effect of attention outside the RFs (i.e., in the opposite hemifield) in only one of
two monkeys. This effect was based on a comparison between two conditions: one in which
attention was directed to a location outside the RF, and one in which attention was directed
inside the RF. Thus, it is unclear whether attention directed outside the RF can shift RFs
compared to those obtained during fixation. Even if the monkey’s attention were directed
toward the peripheral white patch, our results are not out of line with previous studies observing
RF peak shifts with spatial attention (Womelsdorf et al. 2006, 2008).

Retinotopic map in V1

Our derivation of the Polar Log-Gaussian RF model for MT neurons is based on the
complex logarithmic model describing the retinotopic map in V1 (Schwartz 1980).
Representation of the visual world in V1 is organized topographically, with a marked emphasis
on the central visual field. This emphasis has been quantified by measuring the cortical
magnification factor ($M$) expressed as millimeter of cortex per degree of visual angle (Daniel
and Whitteridge 1961). The complex logarithmic model predicts that $M$ is inversely proportional
to eccentricity for linear magnification (i.e., along an isoeccentricity ring or along an isopolar
line).
For squirrel monkeys, a precise retinotopic map of V1 has been constructed from the cortical representation of shadows cast by retinal blood vessels (Adams and Horton 2003). In this study, the linear magnification along isoeccentricity rings ($M_e$) was less than would be predicted from the complex logarithmic model at eccentricities of $>8^\circ$. This is because the V1 surface is oval, and the representations of upper and lower vertical meridia converge at large eccentricities and are not parallel as predicted from the complex logarithmic model. Considering that the macaque V1 also has an oval shape (Van Essen et al. 1984; Horton and Hocking 1996), we expect a similar departure of $M_e$ at eccentricities of $>8^\circ$ for the macaque V1. If the sampling area of MT neurons does not depend on eccentricity, the departure of $M_e$ from the complex logarithmic model should lead to a positive correlation between the RF width along the angular axis ($\sigma_\phi$) and eccentricity in our dataset. We found no such correlation (Fig. 10B). A more detailed RF mapping will help resolve this discrepancy. On the other hand, the linear magnification along isopolar lines ($M_p$) fits well with the prediction of the complex logarithmic model at all eccentricities (Adams and Horton 2003). This suggests that the logarithmic Gaussian function along eccentricity in our Polar Log-Gaussian model is valid for all eccentricities.

Estimates of sampling region

The spatial extent and shape of the sampling region in area V1 from which MT neurons receive input is critically dependent on the model describing the retinotopic map of V1. Results obtained using the complex logarithmic model suggest that the sampling region is elliptical. The short/long ratio of the sampling ellipse was 0.67 (Fig. 10C). The estimated sampling region using the 3-D curved model was more circular than that using the 2-D complex logarithmic model such that the short/long ratio increased to 0.81 (Fig. 11C). This value cannot
be directly compared with the 0.90 in the V4 results because in Motter (2009), the fit on the V1 surface was restricted such that the long radius was forced to be parallel to the meridian line, whereas in our study, either the long or the short radius was forced to be parallel to the meridian line. Our data describing the orthogonal/parallel ratio (median: 0.905) in Figure 11D suggest that MT neurons as a whole integrate information from constant-sized, nearly circular patches of the V1 surface across all ranges of eccentricity.
ACKNOWLEDGMENTS

We thank Sanae Hosotani for technical and surgical assistance and Brad Motter for his assistance in the calculations using the 3-D V1 model.

GRANTS

This work was supported by Grants-in-Aid for Scientific Research on Priority Areas (System study on higher-order brain function) from the Ministry of Education, Culture, Sports, Science and Technology of Japan (18020026 and 20020025) to T. Uka. H. Kumano was supported by a High Technology Research Center Grant from MEXT.
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**FIGURE LEGENDS**

**Fig. 1**

Derivation of a model of an MT neuron RF based on spatial integration of V1 outputs. **A**: A schematic drawing of the retinotopic map in V1. **B**: A hypothetical sampling weight by an MT neuron (Gaussian) is plotted against the V1 retinotopic map along an isopolar direction. Red ticks denote the same eccentricity values as in **A**. **C**: The RF profile of an MT neuron along a radial axis is derived by transforming the Gaussian sampling function onto a linear eccentricity axis. The resulting profile is a log-Gaussian function. **D**: A hypothetical sampling weight of an MT neuron is plotted against the V1 retinotopic map along the isoeccentric direction. Blue ticks denote azimuth. **E**: RF profile of an MT neuron along an eccentricity axis is derived by transforming the Gaussian sampling function onto a linear azimuth axis.

**Fig. 2**

RF mapping procedure and RF location. **A**: Schematic illustration of the RF mapping procedure. A virtual $5 \times 5$ grid (dashed white lines) was positioned to cover the entire extent of the RF of an MT neuron. The center and extent of the grid were adjusted by the initial estimate of the RF. In each trial, a circular patch of random-dot motion is presented at one of the grid locations (dashed red circles). The cyan square denotes the fixation point. **B**: Location and size of RFs of all recorded neurons. Circles show the position and size of the RF of the entire population of MT neurons. The center and the radius of the circle were derived from the best fitting 2-D Gaussian function (Circle model; see Results).

**Fig. 3**

Dataset for a representative MT neuron. **A**: Speed-tuning curve. The curve is the best fit of a
Gamma function. B: Horizontal disparity-tuning curve. The curve is the best fit of a Gabor function. C: Direction-tuning curve. The curve is the best fit of a Gaussian function. D: RF map in 5 × 5 resolution. The mean firing rates are color-coded. The cyan square denotes the fixation point. In A–C, data points and error bars indicate the mean firing rates and SEM, respectively. The horizontal dotted line denotes the spontaneous firing rate.

Fig. 4
RF model fits to the example neuron shown in Fig. 3. The spline RF map is shown at the upper left corner. The $R^2$ values (indicating goodness of fit) for the Circle, the Oriented, the Polar Gaussian, the Cartesian Log-Gaussian, and the Polar Log-Gaussian models were 0.884, 0.896, 0.928, 0.935, and 0.961, respectively.

Fig. 5
More representative MT neurons with RFs best described with the Polar Log-Gaussian model.

Fig. 6
Comparison of the goodness of fit across RF models. A: The $R^2$ value of the Polar Log-Gaussian fit is plotted against the $R^2$ value of the Circle fit for each MT neuron. Median $R^2$ values for the Polar Log-Gaussian fit and the Circle fit were 0.913 and 0.873, respectively. B: The $R^2$ value of the Polar Log-Gaussian fit is plotted against the $R^2$ value of the Oriented fit. The median $R^2$ value for the Oriented fit was 0.886. C: The $R^2$ value of the Polar Log-Gaussian fit is plotted against the $R^2$ value of the Polar Gaussian fit. The median $R^2$ value for the Polar Gaussian fit was 0.908. D: The $R^2$ value of the Polar Log-Gaussian fit is plotted against the $R^2$ value of the Cartesian Log-Gaussian fit. The median $R^2$ value for the Cartesian Log-Gaussian fit was 0.924.
Fig. 7
RF peak shift quantified by nonparametric analysis. A: Analysis procedures for an example MT neuron. For each neuron, the RF peak position was determined from the cubic spline interpolated surface (red dot). Next, the distance from the fixation point (cyan square) to the RF peak was normalized to the distance from the fixation point to the RF center (white square). For this neuron, the normalized RF peak distance was 0.838. The angle difference between the line connecting the fixation point and the RF peak and the line connecting the fixation point and the RF center was then determined. For this particular neuron, the angle difference was –1.69°. B: Polar plot of the normalized RF peak distance and angle difference for the population of MT neurons. The red dot denotes the median values of the normalized distance and angle difference. C: The distribution of the normalized RF peak distances. Filled bars indicate normalized RF peak distances significantly different from one \( (p < 0.05; \text{bootstrap resampling}) \). The median value (filled triangle) was 0.876. D: The distribution of the angle difference. Filled bars indicate angle differences significantly different from zero \( (p < 0.05; \text{bootstrap resampling}) \). The median value (filled triangle) was 0.423°.

Fig. 8
Comparison of RF slopes by nonparametric analysis. A: 1-D slice of the 2-D spline RF map (shown in Fig. 7A) through the fixation point and the RF peak. B: The first derivative of the 1-D slice of the spline RF map. The maximum absolute slope value near the fixation point (magnitude of upward arrow) was compared with the maximum absolute slope value away from the fixation point (magnitude of downward arrow). C: Population data showing the maximum absolute slope value near vs. far from the fixation point. Filled symbols indicate significant
difference between the two values ($p < 0.05$; bootstrap resampling).

**Fig. 9**

RF mapping during motion-direction discrimination. *A*: The psychometric function for an representative experiment in which the proportion of 90° CW choices are plotted against the signed motion coherence of the random-dot motion. *B*: The spline RF map obtained during the fixation task and during the discrimination task are shown along with the associated Polar Log-Gaussian fits. *C*: The $R^2$ values for the Polar Log-Gaussian fit plotted against the $R^2$ values for the Circle fit, the Oriented fit, the Polar Gaussian fit and the Cartesian Log-Gaussian fit. The median $R^2$ values for the Polar Log-Gaussian fit, the Cartesian Log-Gaussian fit, the Polar Gaussian fit, the Oriented fit and the Circle fit were 0.930, 0.931, 0.906, 0.895, and 0.880, respectively. *D*, *E*: The nonparametric analyses of peak shift of RFs obtained during the direction discrimination task. For both panels, the top and bottom histograms show data for the fixation and the discrimination task, respectively, for the same set of neurons. No significant difference was observed between the two task conditions for both the normalized RF peak distance (*D*) and the angle difference (*E*).

**Fig. 10**

RF width parameters for the Polar Log-Gaussian fit. *A*: The width along the radial axis ($\sigma_r$) is plotted against the RF eccentricity for the population of MT neurons. The error bars denote 95% confidence intervals of the fitted $\sigma_r$ calculated using bootstrap resampling. No correlation was found between $\sigma_r$ and eccentricity. *B*: The width along the angular axis ($\sigma_\phi$) is plotted against the RF eccentricity for the population of MT neurons. The error bars denote 95% confidence intervals of the fitted $\sigma_\phi$ calculated using bootstrap resampling. No correlation was found
between $\sigma_{\phi}$ and eccentricity. C: $\sigma_{\phi}$ is plotted against $\sigma_r$. The dashed line denotes the unity slope diagonal. $\sigma_{\phi}$ was significantly larger than $\sigma_r$.

Fig. 11

Analysis of RFs back-projected onto a 3-D V1 surface. A: A diagram of cylindrical coordinates that depict the curved surface of the 3-D model of V1. A point on V1 surface is represented using the distance from the axis of rotation ($r$), the distance from the fovea along the axis of rotation ($z$), and the rotation angle ($\phi$). B: The 3-D model of the V1 surface and the back-projected RF viewed as an orthographic projection. The fovea and far periphery are represented by the leftmost point and the rightmost edge, respectively. The red solid lines represent the back-projected spline RF contour of the representative neuron shown in Figure 3. C: Frequency histogram of the ratio of short/long radii of the 2-D Gaussian function fitted to the back-projected RF contours. The fit was performed such that one of two cardinal axes is forced to be parallel with the meridian line passing through the fovea and the RF mapping grid center. The filled and open triangles denote the median (0.818) and mean (0.810) values, respectively. D: Frequency histogram of the ratio of the radius orthogonal to and the radius parallel to the meridian line. The filled and open triangles denote the median (0.905) and mean (0.947) values, respectively. E: The radius of the Gaussian fitted to the back-projected RF contour is plotted against RF eccentricity. No correlation was found between the two.
Fig. 1

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