MATERIALS AND METHODS

Electrophysiology. We recorded extracellularly from single units in the dorsal LGN, primary visual cortex, and area MT of anesthetized, paralyzed, macaque monkeys (*Macaca fascicularis*). LGN, V1, and MT data were collected from 3, 16, and 13 monkeys, respectively. The numbers of animals for V1 and MT are large because data for this study was collected sporadically during experiments performed for other studies.

Detailed methods for this type of recording are available in Carandini et al. (1997) and O'Keefe and Movshon (1998). Experiments typically lasted 4–5 d during which anesthesia and paralysis were maintained with sufentanil citrate (4–12 $\mu g \cdot kg^{-1} \cdot hr^{-1}$) and vecuronium bromide (Norcuron; 0.1 $mg \cdot kg^{-1} \cdot hr^{-1}$), respectively, administered in lactated Ringer's solution. Infusion solutions were mixed to 2.5% dextrose concentration to provide adequate nutrition, and infusion rate was adjusted to maintain fluid balance ($\sim$4–8 $ml \cdot kg^{-1} \cdot hr^{-1}$). Artificial respiration with a mixture of O_2, N_2O, and CO_2 was maintained with rate adjustments to keep expired P_{CO_2} between 3.8 and 4.0%. Body temperature was maintained near 37°C with a heating pad. EEG and electrocardiogram were monitored to ensure proper depth of anesthesia. The pupils were dilated with topical atropine, and the corneas protected with gas-permeable hard contact lenses. We refracted the eyes with supplementary lenses that were chosen to optimize neuronal responses to high spatial frequencies. All procedures conformed to guidelines of the New York University Animal Welfare Committee.

Tungsten-in-glass microelectrodes (Merrill and Ainsworth, 1972) were advanced with a hydraulic microdrive downward through a craniotomy of diameter 9–10 mm. In some experiments, we used a mechanical microdrive system with quartz-platinum–tungsten microelectrodes (Thomas Recordings, Marburg, Germany). For V1 recordings, the craniotomy was typically centered 4 mm posterior to the lunate sulcus and 10 mm lateral to the midline. For LGN recordings, the craniotomy was centered 7 mm anterior to ear-bar zero and 11 mm lateral to the midline. For MT recordings, the craniotomy was centered 15 mm lateral to the midline, 4 mm posterior to the lunate sulcus, and the angle of advance was 20° down and forward in the parasagittal plane. Action potentials were discriminated using a hardware dual-window time-amplitude discriminator (Bak, Germantown, MD) and time stamped at a resolution of 0.25 msec. Electrolytic lesions were made for histological verification and estimation of cortical layer. V1 neurons were recorded on the operculum and in the calcarine sulcus (typical receptive field eccentricities were 2–5° and 8–24°, respectively). LGN cells were recorded from magnocellular and parvocellular layers at eccentricities ranging from 1 to 23°. MT cells were recorded at eccentricities ranging from 2 to 33° but typically between 3 and 12°. For each cell whose action potential waveform was well isolated from the noise, we ran stimuli as described below.

Visual stimuli. Visual stimuli were generated by custom software on a CRS 2/2 board (Cambridge Research Systems, Kent, UK) under the control of an Intel 86-based host computer. Stimuli were presented on a standard cathode ray tube at a resolution of 1024 × 731 pixels and a video frame rate of 100 Hz vertical refresh, with a mean luminance of 33 cd/m^2. The display was gamma-corrected with a lookup table. We used a front surface mirror to bring the receptive field (RF) of each cell into register with the center of a video monitor placed between 80 and 180 cm from the animal's eye, where it subtended between 10 and 22°. The graphics board that generated our stimulus also generated synchronization pulses that were time-locked to the start of the first frame of our stimulus. These pulses were time-stamped and recorded by the same system used for collecting action potential times.

The RF size was estimated by hand before beginning quantitative characterization with sinewave gratings. Quantitative estimates of RF properties were computed from tuning curves resulting from a series of randomly interleaved stimuli. Responses to drifting sinusoidal stimuli were quantified with DC (mean firing rate minus the baseline rate for a mean gray stimulus) and F1 (amplitude of the Fourier component of the response at the temporal frequency of the stimulus) tuning curves.

For V1 cells, drifting sinusoidal gratings were randomly interleaved under computer control to obtain response tuning curves first for orientation, next for spatial frequency, and then for temporal frequency. Next, we chose the smallest patch of optimized grating that elicited a response easily distinguishable from the spontaneous rate, and we alternated between adjusting the vertical and horizontal position of the patch by hand until the maximal response was obtained. At these coordinates, circular patches of various diameters were interleaved to obtain a tuning curve for size. The classical receptive field (CRF) of the V1 cell was defined to be the smallest circular patch that gave a response no <95% of the maximum.

Cells were classified as simple or complex on the basis of the modulation index computed at the optimal spatial frequency (Skottun et al., 1991). For simple cells, the optimal phase of the grating was subsequently determined from an eight-point tuning curve for static, contrast modulated gratings. For complex cells and MT cells, we quantified directionality using the index $1 - a/p$, where p and a were the responses to preferred direction (that which gave the highest response) and the antipreferred direction (opposite to preferred), respectively, in excess of the spontaneous rate (Maunsell and Van Essen, 1983). Cells were called DS if their directionality was >0.5.

LGN cells were characterized in a manner similar to V1 simple cells with two exceptions. First, LGN cells were mapped with a white noise stimulus in which squares in a 16 × 16 spatial grid were independently assigned zero or maximum luminance on every video frame on the basis of a pseudorandom number generator (Reid et al., 1997). The grid was scaled so that two or three boxes of the grid spanned the center of the LGN RF. A spatial map was computed using reverse-correlation to determine the location, size, and ON or OFF character of the RF center and surround. Second, orientation was set to be vertical (with rightward drift) unless our by-hand characterization or the white-noise spatial map indicated a significant orientation bias. Magnocellular and parvocellular cells (hereafter, m-cells and p-cells) were distinguished using a white-noise stimulus, as described below.

Random sequence stimuli. After the initial characterization of a cell, we studied response timing using random binary and ternary stimulus sequences. For the binary sequences, either the preferred stimulus (P) or the antipreferred stimulus (A) was presented on each video frame (i.e., every 10 msec). The choice between A and P was governed by a pseudorandom sequence generated using the *ran2* algorithm of Press et al. (1992). In later experiments, the randomization was governed by a binary m-sequence (Sutter, 1987; Reid et al., 1997). Ternary sequences, which included a null stimulus (N) were governed by the *ran2* algorithm and consisted of the equiprobable and independent presentation of A, N, or P on each video frame.

For LGN cells, we ran binary sequences with three types of P and A stimuli: spots, annuli, and gratings. (1) Spots: P was a disk of maximum or minimum luminance (for ON or OFF cells, respectively) presented on a gray background and confined to the central region of the RF determined from the reverse-correlation map. A was the disk of opposite contrast to P. (2) Annuli: P was an annulus of maximum or minimum luminance that was confined to the surround determined from the spatial reverse-correlation, and A was the annulus of opposite luminance. (3) Gratings: P was a centered, circular patch of sinusoidal grating having optimal spatial period and phase and covering the RF center and surround. A was counterphase to P, i.e., it had 180° opposite phase.

For V1 simple cells, we used two sets of P and A stimuli. For both sets, P was the optimal sinusoidal grating confined to the CRF (see above), and A was either counterphase or orthogonally oriented to P. We will refer to these two stimuli as the phase and orientation stimuli, respectively. For V1 complex DS cells and for MT cells, P and A were optimal gratings that differed in their direction of movement: P moved in the preferred direction, and A moved in the opposite direction. The amount of movement between video frames was typically 90° of phase but was set to 45° if the cell responded poorly to 90° movements.

LGN m- and p-cells were distinguished on the basis of the presence of contrast gain control (of the type described by Shapley and Victor, 1978) in m-cells and its absence in p-cells (Benardete et al., 1992; Lee et al., 1994; Lee, 1996; Benardete and Kaplan, 1997, 1999; Levitt et al., 2001). Classification was based on the time-domain kernels (Benardete and Kaplan, 1997, 1999) computed for the binary counterphase stimulus and always agreed with our assessment on the basis of contrast sensitivity, transience, temporal resolution, and estimates of the laminar location of the recording.

Data analysis. For all analyses, the times of action potentials were expressed in milliseconds relative to the time at which the raster scan of the video display illuminated the center of the screen, where each neuronal receptive field had been centered. We determined the timing of our stimulus relative to the video synchronization pulses by plotting the luminance at the center of the screen (measured with a photometer) on an oscilloscope that was triggered by the video synchronization pulses. We then measured the timing of our data collection system by passing the video synchronization pulses through the same amplifiers and spike discrimination hardware that we used to detect action potentials. These