

Unequal representation of cardinal vs. oblique orientations in the middle temporal visual area

Xiangmin Xu*[†], Christine E. Collins*, Ilya Khaytin[‡], Jon H. Kaas*[§], and Vivien A. Casagrande*[§]

Departments of *Psychology, ¹Cell and Developmental Biology, and ^IOphthalmology and Visual Sciences, and [‡]Medical Sciences Training Program, Vanderbilt University, Nashville, TN 37232

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A possible neurobiological basis for the "oblique effect" is linked to the finding that more neural machinery is devoted to processing cardinal vs. oblique orientations in primary visual cortex (V1). We used optical imaging to determine whether more territory is devoted to processing horizontal and vertical orientations than oblique orientations in owl monkey middle temporal visual area (MT), a visual area highly sensitive to moving stimuli. We found that more of MT was devoted to representing cardinal than oblique orientations, and that the anisotropy was more prominent in parts of MT representing central vision (≤10°). Neural responses to orientations of 0° and 90° were also greater than those to 45° and 135°. In comparison, an overrepresentation of cardinal orientations in the representation of central vision in owl monkey V1 was relatively small and inconsistent. Our data could explain the greater sensitivity to motion discrimination when stimuli are moved along cardinal meridians and suggest that the neural machinery necessary to explain the motion oblique effect either originates in MT or is enhanced at this level.

oblique effect | optical imaging | orientation preference | owl monkey | visuotopic maps

Primary visual cortex (V1) of primates and a number of other mammals contains a retire to it. mammals contains a retinotopic map of visual space with a map of stimulus orientations superimposed. Neurons selective for similar orientations are clustered together in regions devoted to a portion of visual space. One of the unexpected observations is that more cortical machinery is devoted to representing vertical and horizontal (cardinal) than oblique orientations, because more neurons are selective for cardinal orientations, and cardinal orientations produce a greater neuronal response (1-5). Although the functional consequences of greater representation of cardinal orientations are uncertain, a popular proposal is that such an anisotropy in human visual cortex underlies the ability of humans to better discriminate gratings and other visual stimuli with horizontal and vertical rather than oblique orientations (6-8). This psychophysical observation is known as the "oblique effect," and the effect can be eccentricity-dependent (9, 10). Another proposal suggests that the greater representation promotes the stability of orientation tuning for neurons most sensitive to cardinal orientations, because stimulus adaptation can alter the tuning properties of cortical neurons (11). In either case, differences in the representation of stimulus features in V1 are expected to have significant perceptual consequences.

Surprisingly, there have been no reports about anisotropies in the representation of orientation in primate visual areas outside V1, although few studies have ever investigated this issue beyond V1 (3, 12, 13). Yet there are reasons for believing that orientation anisotropies might be found in other visual cortical areas, especially the middle temporal visual area (MT; also known as V5), because MT receives direct and indirect inputs from V1, and there is a very high proportion of MT neurons that are selective for the direction of motion and the orientation of moving gratings (14). Neurons of similar orientation or direction-of-motion selectivity are clustered into functional columns in MT (15–18). In addition, an oblique effect has been observed in humans for the perception of objects

moving in cardinal vs. oblique directions (7, 19–22). Because of a preponderance of direction-selective neurons, MT is thought to be important to the processing of visual motion (14). Given the columnar arrangement of orientation- and direction-of-motion-selective cells in MT (17, 18), a possible neural mechanism for the oblique effect in motion perception and discrimination could lie in having more cortical space devoted to direction-of-motion-sensitive neurons representing horizontal and vertical orientations rather than oblique orientations in MT.

To test this possibility, we used optical imaging of intrinsic signals to map cortical domains devoted to the representation of different orientations in owl monkey MT. We addressed the following specific questions: (*i*) Does primate visual area MT proportionately or disproportionately represent cardinal and oblique orientations? (*ii*) Does eccentricity affect the proportions of these representations? (*iii*) How do biases for different orientations compare between areas V1 and MT?

Results

Unequal Representation of Cardinal and Oblique Orientations in MT. We examined the organization of orientation preference of MT neurons by activating MT with full screen drifting gratings of different orientations. As shown in Fig. 1 *a*–*c*, orientation domains in MT of owl monkeys were organized very much like those of V1 (23), with clear isoorientation domains (Fig. 1 *a* and *b*) and continuous representation of a series of pinwheels and linear zones (Fig. 1*c*). The average isoorientation domain sizes in MT [0.136 ± 0.075 (mean ± SD) mm², n = 48, measured from three cases], however, are much larger than those in V1 (0.076 ± 0.046 mm²) of owl monkeys (23). Moreover, the MT isoorientation domains consisted of subdomains preferring motion in one direction and the opposite direction (17, 18). These results are similar to those described in previous studies of bush baby and owl monkey MT (17, 18, 24).

To examine whether MT neurons proportionately or disproportionately represent cardinal and oblique orientations, we mapped the amount of MT cortical space devoted to representing different orientations. Specifically, in the orientation preference maps, we examined the distributions of pixels signifying different orientations and assessed the overall relationship between preferred orientations and the amount of cortical space that represented these orientations. For example, in Fig. 1*d*, the histogram shows the pixel distribution of different orientation preferences in the analyzed (encircled) region of Fig. 1*c*, which was produced based upon activation produced by four orientations of drifting gratings that

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Abbreviations: V1, primary visual cortex; MT, middle temporal visual area; AC, area centralis.

[†]Present address: Systems Neurobiology Laboratories, Salk Institute for Biological Studies, La Jolla, CA 92037.

 $^{^{\}mbox{$}}$ To whom correspondence may be addressed. E-mail: jon.h.kaas@vanderbilt.edu or vivien.casagrande@vanderbilt.edu.

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Fig. 1. Orientation preference in owl monkey MT. (*a* and *b*) Orientation difference maps of $90^{\circ}/0^{\circ}$ and $135^{\circ}/45^{\circ}$, respectively. (*c*) Color-coded orientation preference map constructed based on orientation difference maps as shown in *a* and *b*. The color key above *c* codes orientation preference. The dashed lines in *a*-*c* denote the highly responsive MT region. Scale in *a* is 1 mm for *a*-*c*. (*d*) Histogram showing the number of map pixels in the encircled area of *c* representing different orientations. (*e*) Orientation data collapsed into cardinal and oblique angles to show differences in the amount of cortical surface area (i.e., percent cortical space) activated by the cardinal and oblique orientations. P, posterior; L, lateral [case 06.02.2004 (04–25), left hemisphere].

covered 40° of visual space. Overall, there was a tendency for the MT to devote more cortical space to representing cardinal orientations (0°/180°, 90°) compared with oblique orientations (45° and 135°), because Fig. 1*d* has small peaks around the cardinal orientations, with troughs centered near oblique orientations. Further quantification confirmed this. Fig. 1*e* shows the pooled orientation data from Fig. 1*d* for cardinal (0° + 90°) and oblique (45° + 135°) angles, with 53.4% of the cortical space of MT representing cardinal angles and 46.6% of the cortical space representing oblique angles. For the 3 hemispheres examined, we found that orientations were unequally represented in MT to a moderate degree, with 5.6% (±2.4, SD) more cortical space devoted to representing cardinal orientations than oblique ones (see Table 1). This difference reached a statistically significant level (P < 0.005, one-way ANOVA).

We further confirmed this result by comparing the total extent of statistically significant activation by cardinal vs. oblique orientations in single-condition response images. More map pixels with significant activation were associated with cardinal (0° and 90°) than oblique orientations (45° and 135°) (Fig. 5, which is published as supporting information on the PNAS web site).

Given that the oblique effect can be affected by eccentricity (9,

10, 19, 25), and cardinal orientations are overrepresented in the representation of central but not paracentral vision in V1 of some primates (X.X., T. J. Anderson, and V.A.C., unpublished observations), we also compared the magnitude of the anisotropy effect in the central with the peripheral visual field representations in owl monkey MT.

Effect of Eccentricity on the Representation of Orientation. We selectively activated different parts of the visuotopic map of MT by using topographically limited stimuli. As shown in Fig. 2, stimuli restricted to different parts of the visual field activated different regions of MT. Fig. 2 a-c are activation maps produced by using rings centered at the area centralis (AC) with radii of 5°, 7°, and 15°, respectively. In each ring, drifting gratings of two orientations, 0° or 90° were presented and differential activation maps produced with white patches representing one orientation and black the other. Because the stimulus ring was centered on the AC, only the half of the ring in the contralateral visual field activated the imaged MT. The activation pattern in Fig. 1*b* produced by the 7° stimulating ring (inner radius, 7°; thickness, 3°) was used to define the 10° isoeccentricity line. Note that the activation patterns are band-like, as expected for the representations of hemirings in MT (26, 27). In

Table 1. The percentage of MT cortical space devoted to the representation of cardinal and oblique orientations in central (0–10° eccentricity), peripheral (beyond 10° and up to 40°), and both regions of representation

	Central orientations		Peripheral orientations		central plus peripheral orientations	
Case no.	Cardinal (0° + 90°), %	Oblique (45° + 135°), %	Cardinal, %	Oblique, %	Cardinal, %	Oblique, %
03.16.2004	58.0	42.0	50.2	49.8	51.4	48.6
10.27.2003	54.1	45.9	52.5	47.5	53.6	46.4
06.02.2004	53.0	47.0	52.7	47.3	53.4	46.6



Fig. 2. Visual field maps. a-c are from one case (case 03.16.2004, left hemisphere), and d-f are from a second case (case 03.02.2004, right hemisphere). (a-c) Activation maps produced by using drifting gratings inside rings of different widths (a, 1.5°; b and c, 3°) centered at the AC with radii of 2.5°, 7°, and 15°, respectively. These activation patterns were produced by drifting gratings of orientation 0° and 90° inside the rings. The dark and white patches are areas responding to each of the two orientations, i.e., representing orientation modules that are strongly responsive to 0° and 90°, respectively. (d-f) Activation maps produced by using drifting gratings of different sizes (d, 5° radius; e, 10° radius; f, 20° radius) centered at AC, respectively. A anterior; L, lateral. (Scale bar, 1 mm.) Please note that the maps of a-c were obtained from the left hemisphere, and those of d-f were from the right hemisphere, so that the two sets of maps appear to be mirror images.

addition, as the rings changed from central to peripheral visual field positions, the activated patches progressed from posterior to anterior parts of MT. Similarly, Fig. 2 *d*–*f* are activation maps produced by using drifting gratings inside circles of different sizes [5° radius (*d*) and 10° radius (*e*), and 20° radius (*f*)] centered at the AC. Successively larger stimuli activated successively larger arrays of patches. Overall, as demonstrated in our previous study in bush baby MT (18), these results indicate the existence of an orderly retinotopic map in owl monkey MT. Once the visuotopic organization of MT was established, central MT was defined as the sector representing 0–10° eccentricity, and peripheral MT was defined as the sector representing >10–40° eccentricity (stimuli beyond 40° were not presented).

Next, we compared the proportions of cortical territory devoted to different orientations in central and peripheral MT. We found that the unequal representation of cardinal and oblique orientations was much more prominent in central MT representing 0-10° than that in peripheral regions $(>10-40^\circ)$ of MT. For example, in Fig. 3d, the histogram shows the pixel distribution of orientation preferences in central MT, in which there are clear peaks near the cardinal orientations (0°/180°, 90°) and valleys around the oblique orientations (45° and 135°). The larger representation of cardinal orientations also can be seen in Fig. 3 e and f. The orientation data collapsed around each of the four orientations (0°, 45°, 90°, and 135° $\pm 22.5^{\circ}$) shows the amount of cortical space representing different orientations in central MT (Fig. 3e), and that the percentage of cortical space activated by cardinal orientations ($\overline{0}^{\circ}$ and $9\overline{0}^{\circ}$) is greater than that for oblique orientations (45° and 135°). Fig. 3f shows the pooled orientation data for cardinal $(0^{\circ} + 90^{\circ})$ and oblique $(45^{\circ} + 135^{\circ})$ angles, with 58% of the cortical space representing cardinal angles and 42% of the cortical space representing oblique angles. In contrast, the representations of cardinal and oblique orientations in the representation of peripheral vision in MT were nearly equal. Fig. 3 g-i show histograms of the distributions of pixels in relation to orientation preference, the orientation data collapsed around each of the four orientations, and the pooled orientation data for cardinal and oblique angles, respectively, for peripheral MT. For peripheral vision $(10-40^\circ)$ in this case, 50.2% of the cortical space represented cardinal angles, and 49.8% of the cortical space represented oblique angles.

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As also shown in Table 1 and Fig. 6, which is published as supporting information on the PNAS web site, the overrepresentation of cardinal vs. oblique orientations across cases was strong in the central vision representation but weak in the peripheral vision representation in MT, although there was a noticeable degree of variability across the animals. On average, our data showed that $10.1 \pm 5.3\%$ (SD) more cortical space in central MT was activated preferentially by cardinal orientations compared with oblique orientations (P < 0.003, one-way ANOVA). A much weaker preference existed in peripheral MT, with $3.6 \pm 2.8\%$ (SD) more cortical space activated by cardinal orientations (P = 0.04). This result is compatible with previous reports suggesting that an oblique effect exists only for eccentricities up to $\approx 10^{\circ}$ and is essentially undetectable at greater eccentricities (9, 10, 28).

Intrinsic Signal Strength of the Cardinal vs. Oblique Orientations. We also found that the amplitude of the evoked intrinsic signal in MT was greater for cardinal than for oblique stimuli in the two cases examined. As shown in Fig. 4, the two curves show the time courses of intrinsic signal strength for the 90° (red) and 135° (black) orientations in central MT in response to 8 sec of stimulation (indicated by the black solid line above the x axis) by using full-field $(64^{\circ} \times 72^{\circ})$ drifting gratings in one representative case. Each curve represents the average signal strength (mean \pm SD) from highly responsive isoorientation domains, plotted against the baseline (no stimulus, blank control). The x axis shows time in seconds, and the y axis shows intrinsic signal strength, i.e., the change in intensity of optical reflectance relative to the baseline ($\Delta R/R$). In Fig. 4, the $\Delta R/R$ peaked at 8 sec after stimulus onset. The peak $\Delta R/R$ for orientations 90° and 135° was $-0.130 \pm 0.026\%$ (SD), and $-0.094 \pm 0.027\%$, respectively. Nonparametric statistical analysis showed that the magnitude of optical responses to the 0° and 90° orientations differed from that to orientations of 45° and 135°, because the median $\Delta R/R$ amplitude for orientations 0° and 90° was greater than for orientations 45° and 135° (-0.081% vs. -0.071%; Mann–Whitney U test, P < 0.001). Examination of statistically significant responses in single condition maps demonstrated the same trend across MT. As shown in Fig. 5 for one representative case, the response amplitudes of pixels with significant activation were higher for cardinal orientations than for oblique ones (pooled test for significantly activated pixels with orientations 0° and 90° vs. orientations 45° and 135°, Mann–Whitney U test, P < 0.0001), and the median amplitude values were -7.24×10^{-4} , -5.94×10^{-4} for cardinal orientations (0° and 90°) and oblique orientations (45° and 135°), respectively.

Source of the Orientation Representation Bias. Considering that MT receives direct and indirect inputs from V1 (29), we wondered whether V1 might be the source for the MT bias of orientation representation. Thus, we compared the orientation representation



Fig. 3. Orientation maps at central and peripheral eccentricities in MT. (*a* and *b*) Surface image and orientation difference image (90°/0°), respectively. The encircled area was used for subsequent analysis. (*c*) Portion of the color-coded orientation preference map, superimposed on the cortical surface image (*a*). The color key for different orientation preferences is above. The white dashed line in *c* divides the analyzed MT region into areas representing central ($\leq 10^\circ$) and peripheral visual fields (beyond 10°), based upon the visuotopic mapping shown in Fig. 2 *a*–*c*. (*d*) Histogram showing the pixel distributions in relation to different orientation preferences in central MT. There are peaks near the cardinal orientations (0°/180°, 90°) and valleys around the oblique orientations (45° and 135°), indicating that more cortical space responded best to gratings at the cardinal axes compared with those at oblique angles. (*e*) Orientation data collapsed around each of the four orientations (0° + 90°) and oblique (45° + 135°) angles. (*g*–*i*) Histogram of the pixel distribution in relation to orientation preference, the orientation data collapsed around each of the four orientations, and the pooled orientation data for cardinal and oblique angles, respectively, in peripheral MT (case 03.16.2004).

in owl monkey V1 with that of MT in the equivalent of the central vision representation in MT (0–10°). Areas of V1 representing peripheral vision were not visible to the camera, because they lie on the medial wall of the hemisphere. Table 2 shows the percentage of cortical area devoted to the representation of cardinal and oblique orientations in V1 (eccentricities estimated <10°) across different owl monkeys. The percent difference in the amount of V1 cortical space representing cardinal and oblique orientations ranges from -3.4% to +5.6% across these cases, although the more central portion of V1 could have a larger anisotropy [e.g., see case 03.19.02 (eccentricities mapped $\leq 5^\circ$) in Table 2]. Overall, we found only a small overrepresentation (1.6 \pm 3.2%) of cardinal orientations in V1 at these eccentricities. Given that central MT (0–10°) shows a

Table 2. The percentage of cortical space devoted to the representation of cardinal and oblique orientations in owl monkey V1 (eccentricity estimated $\leq 10^{\circ}$)

Case no.	Cardinal orientations ($0^{\circ} + 90^{\circ}$), %	Oblique orientations (45° + 135°), %
12.12.01	51.2	48.8
01.15.02	51.5	48.5
02.26.02	49.6	50.4
03.19.02	52.8	47.2
04.16.02	48.3	51.7
12.10.02	51.3	48.7

large and consistent difference in the representation of cardinal over oblique orientations, the anisotropy in the orientation representations in MT may not completely depend on a relay of the anisotropy from V1, unless the neurons projecting to MT differ in orientation preference from the population in V1. Thus, some of the anisotropy in MT appears to originate in MT.

Discussion

In the present study, we used optical imaging of intrinsic signals to provide evidence that the MT of owl monkeys devotes more cortex to cardinal orientations than oblique orientations. The finding that cardinal orientations have a greater representation than oblique orientations in an extrastriate visual area of a primate is previously uncharacterized. MT is one of the visual areas, in addition to V1, and the second visual area, V2, which is known to systematically represent the orientation of visual stimuli in primates. In these areas, across the surface of cortex, neurons systematically vary in orientation preference. Within V1 of primates and cats, cardinal orientations are overrepresented compared with oblique orientations in that more neurons prefer cardinal orientations, and cardinal orientations produce a stronger neuronal response (1-4). Although some have proposed that this enhanced representation in V1 is responsible for the "oblique effect" (the observation in human psychophysical studies that detection of oriented stimuli is more sensitive for cardinal than oblique orientations), data from other studies showing prominent oblique effects with pattern components that are $>10^{\circ}$ apart suggest that the small receptive fields of V1

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neurons are not responsible, and that some oblique effects originate in "higher" visual areas (8). Additionally, the demonstration of a prominent oblique effect in visual motion perception suggests that higher visual areas, such as area MT, contribute to this perceptual anisotropy (7).

Our present finding of a greater representation of cardinal orientations in MT supports previous proposals (7, 8) that the oblique effect may originate from neural machinery located central to V1 (also see ref. 13 for related data in cats), even though V1 does show a greater representation of cardinal over oblique orientations in some species (5, 30, 31). The present results indicate that MT overrepresents cardinal orientations both in the proportion of the orientation map and in the magnitude of the neural response. Furthermore, this disproportionate representation is also greater in the part of MT representing central visual field locations $(10-40^\circ)$.

Our data indicating that orientations are unequally represented in MT suggest an explanation for the behavioral finding that humans have a greater sensitivity to motion in cardinal directions than in oblique directions (7, 19-22). Because neurons in MT are highly selective for both direction of motion and stimulus orientation, orientation specific differences in motion perception could be mediated, at least in part, by neurons in MT. Because our stimuli were moving gratings of given orientations, we did not disentangle a possible anisotropy in the representation of orientation from one in direction of motion. Although this could have been sorted out by stimulating MT by using drifting dots, drifting dots produced only weak optical signals in comparison to full-field grating stimuli. Orientation domains in MT include smaller direction of motion domains, but the amplitude of orientation maps is several times higher than that of direction maps (17). Thus, we measured orientation domains. Nevertheless, given that nearly all MT neurons are responsive to motion orthogonal to their preferred orientations (17, 32-34), the number of neurons tuned to cardinal directions of motion should also be disproportionately large. Indeed, inspection of the published maps of direction preference domains in MT of bush babies (18) and owl monkeys (17) suggests a greater representation of cardinal directions.

Besides the oblique effect, another effect, the radial orientation effect, has been reported in the literature (35). Physiologically, microelectrode recordings have found a radial bias in the distribution of preferred directions in MT and in the lateral suprasylvian gyrus of the cat (36, 37). Particularly, for macaque MT neurons, there is a prominent anisotropy for directions oriented away from the center of gaze, but this anisotropy is present only among neurons with peripherally located receptive fields (36). In addition, a recent study confirmed a robust radial orientation bias throughout visual cortex by using human psychophysics, and human and monkey fMRI; although the neural mechanisms for the oblique effect and the radial orientation effect may be different (35), both the present study and previous studies point out that there are underlying links between orientation and visuotopic representations (35). Furthermore, some studies suggest that both the cardinal vs. oblique anisotropy, and the radial vs. tangential one constitute a characteristic structural property of the visual system (28).

The results do not indicate how the overrepresentation of cardinal orientations is created in MT. It seems likely that some of the effect may be relayed from V1, which projects directly and indirectly to MT (29). In owl monkeys, lesions and deactivations of V1 rendered MT unresponsive to visual stimuli (24, 38). However, reanalysis of the orientation preference maps from our previous study revealed only a small and inconsistent overrepresentation of cardinal orientations in the region of V1 representing 0–10° eccentricity in owl monkeys, whereas more peripheral portions of V1 were unavailable for imaging (23). In the bush baby a consistent anisotropy was found in V1 by using optical imaging but only for the 0–3° representation and not beyond this eccentricity (X.X., T. J. Anderson, and V.A.C., unpublished observations). We may find



Fig. 4. Intrinsic signal strength of the cardinal vs. oblique orientation responses. The two curves show the time courses of intrinsic signal strength for 90° (red) and 135° (black) orientations in central MT in response to 8 sec of stimulation (indicated by the black solid line above the *x* axis) by using full field $(64^{\circ} \times 72^{\circ})$ drifting gratings. Each curve represents the average signal strength (mean \pm SD) from five isoorientation domains, plotted against the baseline (no stimulus, blank control). The domains for 90° and 135° were adjacent to each other and selected from the same region of interest. The *x* axis shows time in seconds, and the *y* axis shows intrinsic signal strength, i.e., the change in intensity of optical reflectance relative to the baseline (case 03.16.2004).

that a consistent anisotropy also exists at this more central visual field location in owl monkeys, but this still does not account for the consistent anisotropy found for larger eccentricities extending beyond 3° in MT. Therefore, the present observations support the possibility that any overrepresentations of cardinal orientations relayed from V1 are enhanced in MT, possibly by anisotropies in the pattern of diverging and converging cortical inputs, as well as intrinsic circuits. If a consistent difference in the V1 and MT orientation maps does exist, and this is also the case for other primates, including humans, we would expect a greater oblique effect for moving, oriented than for static stimuli, because moving stimuli would more effectively engage MT neurons and the greater representation of cardinal orientations is more pronounced in MT than in V1. The greater representation of neurons devoted to cardinal orientations in MT may also be reflected in those neurons being less susceptible to stimulus-induced plasticity, as suggested by Dragoi et al. (11).

Materials and Methods

General Preparation. Four adult owl monkeys (*Aotus trivirgatus*) of both sexes were used in this study. All animals were handled according to an approved protocol from the Vanderbilt University Animal Care and Use Committee. Animals were prepared for surgery, paralyzed, and anesthetized as described elsewhere (18, 23, 24, 39). Five hemispheres were imaged in this study; three of them yielded high-quality functional maps. Some data from these animals were presented previously in abstract form,** and part of the data reported here was used for a separate analysis in an earlier paper (24).

Optical imaging and analysis, visual stimuli, and histological reconstruction procedures were performed as described in detail in previous studies (18, 23, 24, 39). Briefly, intrinsic optical imaging signals were acquired with the Imager 2001 differential video-enhancement imaging system and VDAQ/NT data acquisition

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software (Optical Imaging, Mountainside, NJ). For visuotopic mapping, spatially limited horizontal and vertical grating stimuli were presented monocularly within either circular patches, rings, or bars at eccentricities ranging from 0° to 40° (see ref. 18 for details). We used monocular stimulation to map the visual field representation to avoid possible artifacts because of misalignment between the two eyes of the animal. To study the functional organization of orientation preference, high-contrast rectangular gratings (fundamental spatial frequency, 0.5 cycles per degree; drift velocity, 2 Hz; contrast, 100%; duty cycle, 20%) of four orientations were displayed on the full screen $(64^\circ \times 72^\circ)$ and presented through both eyes. Binocular stimulation produced patterns of orientation responses identical to those of monocular stimulation but with stronger cortical activation. In orientation tests, all four orientation conditions were presented in a randomized order. To construct orientation difference maps, we summed together all images associated with the same orientation by using Winmix software (Optical Imaging). The summed images acquired during the presentation of one orientation were divided by the summed images acquired during the presentation of the orthogonal orientation to create orientation difference images. All four orientation difference images were also combined to produce orientation preference maps by vector summation, in which the orientation preference is colorcoded. In addition, all images associated with stimuli of one orientation at a specified position were summed and divided by the images associated with the orthogonal orientation at the same position to create visuotopic maps. Once visuotopic relationships were identified, the central region of MT was defined as the sector representing the visual field from 0° to 10° eccentricity. The peripheral region was defined as the sector of MT representing everything beyond 10° eccentricity.

Quantitative Measurements. To examine the intrinsic signal strength, we measured the intensity of optical reflectance (R)during the stimulus condition relative to the intensity during the blank control ($\Delta R/R$), by using raw data frames. To examine intrinsic signal magnitudes in response to orientations, we specifically recorded all frames for prestimulation, stimulation, and interval periods [e.g., 4-sec blank control, 8-sec drifting grating stimulation plus 12- or 13-sec stimulus interval (blank screen)]. Video frames were summed together to produce data frames (1 sec for a data frame) to estimate optical reflectance changes. The blank gray conditions were set at the average light intensity of the stimulus conditions, with a mean luminance of 30 cd/m^2 . Given that reflectance changes peaked $\approx 8 \sec$ (frame 12) after stimulus onset (see Fig. 3), we calculated $\Delta R/R$ as [average (frame 10 to frame 14)] - blank control frame]/blank control frame \times 100%. We averaged $\Delta R/R$ across map pixels of 5–10 specific isoorientation domains from 10 to 15 different trials. We also used raw data frames to analyze single-condition response images and examined both the total extent of statistically significant activation and peak ampli-

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tudes of significant responses (4, 40). Specifically, we carried out paired t tests across 10-15 different trials by comparing the stimulation condition at each individual orientation (average response images across frames 10-14) with the baseline activity of blank screen (average baseline images across frames 1-4) on a pixel-bypixel basis. The level of significant activations was determined at $P \le 0.05$; then response magnitudes of statistical significant pixels were evaluated for statistically significant responses. Fig. 5 illustrates the statistical P value maps and response magnitude maps resulting from these analyses. The map pixels with significant activation in the statistical P value maps showed a good match with the highly responsive domains of single orientations in the orientation difference maps (see Fig. 5).

To assess the amount of cortical area devoted to all orientations in different regions of MT, we examined pixel distributions of orientation preference maps at different orientations and assessed the overall relationship between preferred orientations and amount of cortical space that represented these orientations (refs. 30 and 31; see, e.g., Figs. 1d and 3d). The orientation preference maps were chosen for this analysis, because they give a better indication of the area of cortex that preferred a given orientation than the orientation difference maps (30, 31). To determine whether a greater amount of cortex was devoted to the cardinal orientations (0° and 90°) vs. the oblique orientations (45° and 135°), data from the orientation distribution histogram were collapsed around each of the four orientations (0°, 45°, 90°, and 135° \pm 22.5°) into the pooled distributions for cardinal and oblique orientations examined for each eccentricity (e.g., Fig. 3e and f). In addition, we reanalyzed the orientation preference maps of owl monkey V1 from our previous study (23) to assess the amount of cortical area devoted to each orientation in the region of V1 representing the central 0-10° of visual space (see Table 2), to compare the orientation representation in owl monkey V1 with that of MT.

We also measured isoorientation domain sizes from orientation difference images (e.g., $0^{\circ}/90^{\circ}$ and $45^{\circ}/135^{\circ}$) of owl monkey MT. The same region of interest (ROI), relatively free of blood vessels, was chosen for all four orientation difference images of the same case with matched peak signal strength. Then the ROI of each image was thresholded to include only the top 10-20% darkest pixels to acquire isoorientation domain contours for quantitative measurements. The Image Processing Toolkit (Reindeer Graphic Company, Raleigh, NC) was used to measure the domain sizes.

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