The Organization of the Middle Temporal (MT) Visual Area in Owl Monkeys Revealed by Optical Imaging

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1. Introduction

Area MT has been studied in a variety of primates since its discovery in the early 1970s (Allman & Kaas, 1971). There is general agreement that MT is part of the hierarchy of dorsal visual areas and is important in processing complex motion. Aspects of the organization of MT, however, remain controversial, including whether properties such as orientation are mapped the same way in MT across species and whether a global retinotopic map can be demonstrated in MT. Given these controversies, we examined MT using optical imaging of intrinsic signals.

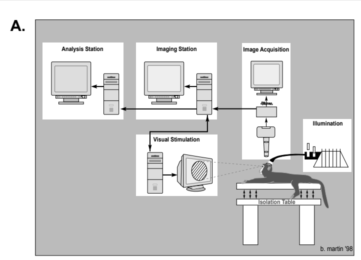
2. Questions

- Does an orderly, global retinotopy exist in area MT of Owl Monkeys?
- What is the point spread and cortical magnification factor in owl monkey MT?
- How does the functional organization of owl monkey MT compare with the organization of MT in other primate species?

3. Methods and Materials

The four owl monkeys used in this study were handled according to an approved protocol from the Vanderbilt University Animal Care and Use Committee. Prior to surgery, animals were paralyzed and anesthetized as described in Xu et al. (2001, 2004). Paralysis and anesthesia were maintained by intravenous infusion of vecuronium bromide (0.1-0.3 mg/kg/hr) mixed in 5% dextrose lactated Ringer's, sufentanil (15-20 ug/kg/hr) and Propofol (2,6,-di-isopropylphenol: 4-7 mg/kg/hr). In order to ensure that adequate levels of anesthesia were maintained throughout the experiment, heart rate, peak end tidal CO_2, and temperature were monitored continuously after paralysis and the level of anesthetic increased if necessary. Pupils were dilated with atropine eye-drops and clear gas permeable contact lenses were used to render the retina conjugate with the viewing screen at a distance of 28.5 cm. Lenses with 3mm artificial pupils were used. An opening was made in the skull over MT and was sealed with 1% agarose under a cover glass.

Intrinsic optical imaging signals were acquired with the Imager 2001 differential video-enhancement imaging system and VDAQ/NT data acquisition software (Optical Imaging Inc.). Reference images of cortical vasculature were acquired with a 540 nm green light. The cortex was illuminated with a 611 nm light during data acquisition. For functional mapping of MT, we used either moving full field gratings or retinotopically restricted stimuli. Each stimulus contained square wave gratings with a fundamental spatial frequency of 5 cycles/deg and a drift velocity of 10 deg/sec. These parameters were shown to be optimal for area MT during pilot experiments. Full field gratings were presented at four orientations.



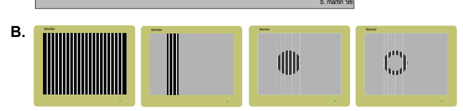


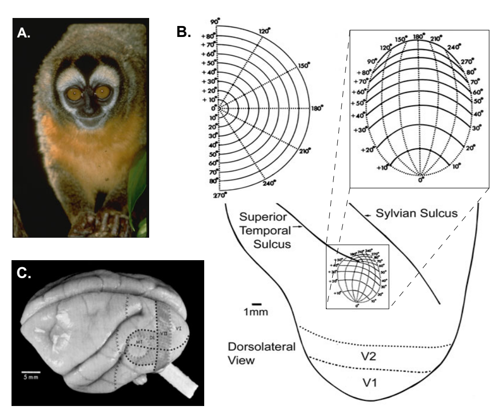
Figure 1.
A. Optical imaging setup. **B.** Examples of the stimuli used.

3. Methods and Materials (cont.)

To determine retinotopic relationships, gratings were presented at two orientations inside circular windows (1 - 40 deg diameter), vertical and horizontal rectangular windows (0.3 - 5 deg along smallest dimentions), or annular windows (0 - 20 deg radius and 0.3 - 5 deg wide)) placed at various eccentricities. Video images were acquired at a rate of 30 frames/sec, but all frames acquired for each condition during the 8-sec period of stimulation were summed together for 8 data frames before further analysis. These data acquisition periods were followed by 17 sec. interstimulus intervals. Stimulus sets were repeated 10 - 30 times. Analysis was done using WinMix (Optical Imaging Inc.) and custom Matlab (MathWorks Inc.) programs. The summed images acquired during the presentation of one orientation were divided by the summed images acquired during presentation of the orthogonal orientation to create differential maps of orientation preference (difference images) (Blasdel, 1992; Bosking et al., 1997). Resulting difference images were smoothed using a 6 x 6 pixel mean filter kernel. Low frequency noise was reduced by convolving the image with a 60 x 60 pixel mean filter kernel and subtracting the result from the original image. Vector summation of the difference images was done on a pixel by pixel basis to create an orientation preference (angle) map, in which preferred orientations were represented with colors, a magnitude (vector strength) map, in which degree of overall orientation selectivity was represented by brightness, and a polar map, which is a combination of angle and magnitude maps (see Bosking et al., 1997 for details). To obtain quantitative measurements of the activation domain sizes in response to retinotopically restricted stimuli, an Image Processing Tool Kit (Reindeergraphics) was used. Areas of activation were defined as areas with pixel intensities of more then 1.5 - 2 STD higher then the mean.

At the termination of each experiment, the owl monkey was deeply anesthetized with an overdose of sodium pentobarbital and perfused transcardially with 0.9% saline in 0.1M phosphate buffer (PB) followed by 2% paraformaldehyde in 0.1 M PB. The brain was removed and the cortex was separated and flattened. The cortex was frozen and cut with the surface vascular pattern preserved in the first 100 - 150 µm section. Sections were processed for cytochrome oxidase (CO) and myelin. Area MT is defined by its dense CO and heavy myelin stains. Surface and radial blood vessels were the primary landmarks used to align histological sections to the resultant images. Distortion due to tissue shrinkage were handled by global scaling and rotation.

Figure 2.
(A) Owl monkey (*Aotus trivirgatus*). **(B)** Depiction of owl monkey MT as defined by electrophysiological recording (from Allman & Kaas, 1971). Top row - image of a visual hemifield and its representation in MT. Numerals indicate degrees. Bottom row - illustration of MT location and topography in relation to known landmarks. Note that the brain is rotated in this view such that ventral is to the left and posterior to the bottom of the figure. **(C)** Owl monkey brain with area MT outlined and neighboring visual areas defined as follows: the dorsal lateral (DL/V4) area and the secondary (VI) and primary (VII) visual areas (from Allman & Kaas, 1974).



4. Results

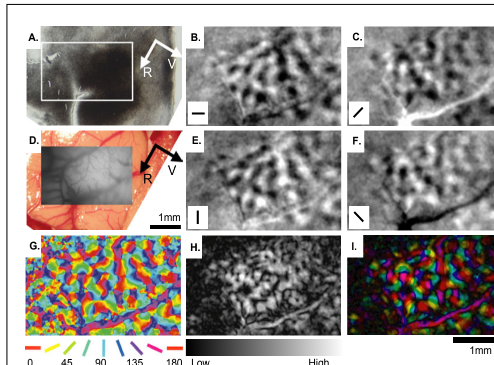


Figure 3.
Functional maps of area MT. **(A)** Myelin stained section showing heavy myelination in and around MT. White rectangle represents studied area. R-rostral; V-ventral. **(D)** Green light reference image of the cortical surface showing vascular pattern used to align optical images with histological sections. Reference image is aligned with color photo of the cortical surface. Differential images of orientation preference **(B, C, E, F)**, with the orientation of the darker patches indicated at the lower left corner of each panel. **(G)** Orientation preference map obtained by vector summation of maps in **B, C, E, F** with color key shown below. **(H)** Magnitude map showing strength of activation across MT, with key shown below. **(I)** Polar map showing both orientation preference and magnitude of activation.

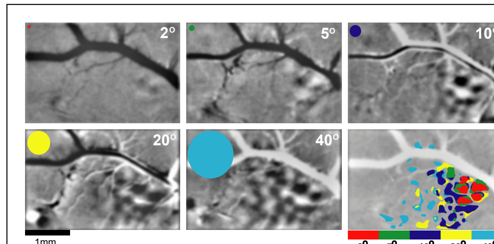
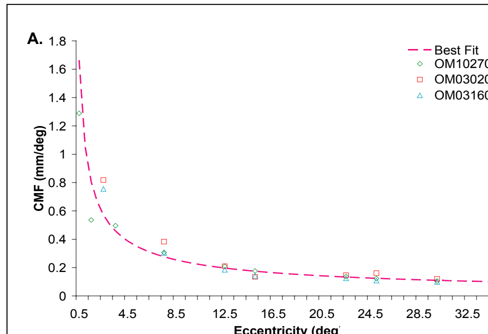


Figure 4.
Activation of MT by 0/90 degree gratings inside a circular window centered on the *area centralis*. Stimulus diameter is shown in the upper right corner of each image. The relative size of individual stimuli is indicated by circles in the upper left corner. Bottom right image is a summary image, demonstrating the relative size of activation produced by indicated stimuli.

4. Results (cont.)



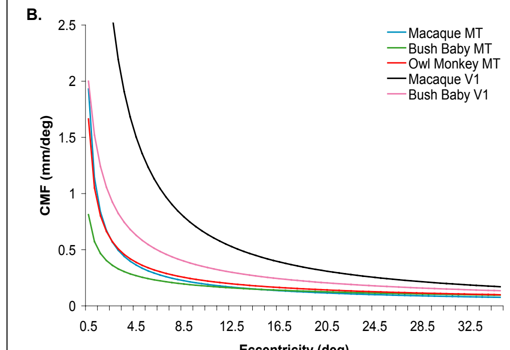


Figure 5.
(A) Linear cortical magnification factor (CMF) measured in three hemispheres. The power function that best fits data is $1.051*(\text{Eccentricity})^{-0.663}$. **(B)** Plot of linear CMF as a function of eccentricity (E) for the following species:

owl monkey	(red line)	$CMF = 1.051*E^{-0.663}$	(Present study)
macaque MT	(blue line)	$CMF = 1.14*E^{-0.76}$	(Albright & Desimone, 1987)
bush baby MT	(green line)	$CMF = 0.573*E^{-0.504}$	(Xu, et al., 2004)
macaque V1	(black line)	$CMF = 10.1*(E+0.82)^{-1.14}$	(Van Essen et al., 1984)
bush baby V1	(pink line)	$CMF = 2.36*(E+ 0.73)^{-0.8}$	(Rosa et al., 1997)

In central vision, the CMF of owl monkeys is very close to one obtained for macaque monkeys and is larger then the CMF obtained for bush babies. Note that, due to the anisotropic representation of the horizontal compared to the vertical meridian (see Figure 6), the CMF obtained in this study represents the average CMF at any given eccentricity.

4. Results (cont.)

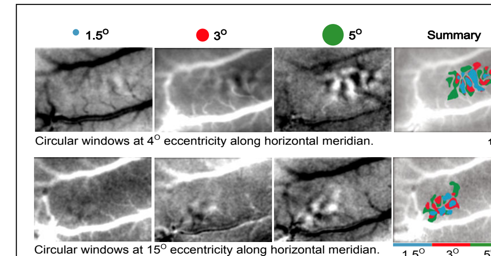


Figure 6.
Point spread activation produced from circular stimulus patches of 1.5, 3, and 5 degrees in diameter at 4 degrees eccentricity (top row) and 15 degees eccentricity (bottom row) presented along the horizontal meridian. Activation demonstrates clear asymmetry with an aspect ratio of 1.5-1.9 to 1.0 of the horizontal to the vertical spread of activation.

5. Conclusions

- Owl monkey MT shows an orderly representation of the visual field at both the global and local level.
- Like V1, orientation in area MT is organized into pinwheels and linear zones.
- Central vision has a greatly magnified representation in owl monkey MT and there is a 1.5-1.9/1.0 anisotropy in the representation of the horizontal/vertical meridians.
- Species comparisons show that the cortical magnification factor is greater for owl monkeys than for bush babies and is more similar to that of macaque monkeys.
- Taken together with previous findings, our results demonstrate that the basic organization of area MT is similar across primates. Differences seen appear to reflect differences in emphasis on central vision in different primates.

6. References

Albright TD, Desimone R, (1987). Local precision of visuotopic organization in the middle temporal area (MT) of the macaque. Exp. Brain Res. 65: 582-592.
Allman JM, Kaas JH, (1971). Representation of visual field in caudal third of middle temporal gyrus of owl monkey (Aotus trivirgatus). Brain Res. 31: 81-105.
Allman JM, Kaas JH, (1974). A crescent-shaped cortical visual area surrounding the middle temporal area (MT) in the owl monkey (Aotus trivirgatus). Brain Res. 81: 199-213.
Blasdel GG, (1992). Differential imaging of ocular dominance and orientation selectivity in monkey striate cortex. J. Neurosci. 12: 3115-3138.
Bosking WH, Zhang Y, Schofield B, Fitzpatrick D, (1997). Orientation selectivity and the arrangement of horizontal connections in tree shrew striate cortex. J. Neurosci. 17: 2112-2127.
Rosa MGP, Casagrande VA, Preuss T, Kaas JH, (1997). Visual field representation in striate and prestriate cortices of a prosimian primate (Galago garnetti). J. Neurophys. 77: 3193-3217.
Van Essen DC, Newsome WT, Maunsell JHR, (1984). The visual field representation in striate cortex of the macaque monkey: asymmetries, anisotropies, and individual variability. Vision Res. 24: 429-448.
Xu X, Ichida JM, Allison JD, Boyd JD, Bonds AB, (2001). A comparison of koniocellular, magnocellular and parvocellular receptive field properties in the lateral geniculate nucleus of the owl monkey (Aotus trivirgarus). J Physiol. 531: 203-218.
Xu X, Collins CE, Kaskan PM, Khaytin I, Kaas JH, Casagrande VA, (2004). Optical imaging of visually evoked responses in prosimian primates reveals conserved features of the middle temporal visual area. PNAS 101: 2566-2571.

7. Acknowledgements

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