Human MT complex: selectivity to motion flow stimuli and to retinotopic and spatiotopic input

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INTRODUCTION & AIM

Many neurons in the macaque visual cortex have receptive fields that are affected by gaze direction. Population of neurons with spatiotopic receptive fields have been found in parietal areas that tend to serve polysensory functions (VIP – V6) where the remapping is needed to integrate different sensory inputs (Sereno, 2006; Bremmer et al., 2001; Duhamel et al, 2002-2005). In human and monkey, neurons of associative visual cortical areas have transiently spatiotopic receptive fields that remap their spatial position during saccadic eye movements (Nakamura & Colby, 2002; Duhamel, Colby Goldberg, 1992; Merriam, Genovese, Colby, 2003 Melcher, 2005). Psychophysical evidences have shown a linear integration over time for weak motion signals presented at different retinal location but identical spatial position, indicating the existence of a spatiotopic mechanism that integrates motion signal at threshold (Melcher & Morrone, 2003). These data are in agreement with recent fMRI data (D'Avossa et al, Nature Neuroscience 2007) that demonstrated the existence of a region within MT complex with a spatiotopic selectivity. However they contrast with the result of Garden et al (2008, J Neuroscience) that showed that MT (and many other occipital cortical area) represent the stimuli manly in retinotopic coordinate with a small or absent gaze modulation. The aim of the present work is to understand whether the portion in MT complex that shows spatiotopic properties does belong to the retinotopic portion of MT and its specificity to the flow motion.

MATERIAL AND METHODS

Different block-designed stimuli were used for the retinotopy, the motion localizer and the spatiotopic selectivity. Vertical and horizontal meridians were identified presenting moving dots in two opposing sectors (+-18° degree angle) along the 2 principal meridians. Each sector covered +- 18° of visual angles and extended from the screen centre (corresponding to the fixation point) to +-7.5° of eccentricity. Each stimulus was presented for 15 s and a total of 12 repetions in each scan. To identify the areas corresponding to the four visual quadrants, moving dots (expanding/contracting) were presented within 4 circular sectors subtending +-40° of visual angle centred along the +-45° orientation. The quadrantis stimuli were presented sequentially in a clockwise order for a total of 4 repetitions in each scan. For the MT localizer, the sequence consisted of 18 s blocks alternating between random and coherent motion. Three types of coherent motion were used: translation, rotation or flow fields that changed gradually from pure expansion, to inward spiral, clockwise rotation, spiral, contraction, and so on. Both for the retinotopy and the localizer stimuli, the dots moved along trajectories with a constant speed of 4.5°/sec and a limited lifetime of 20 frames (333ms) both for the coherent and the noise stimuli (Morrone et al., Nature Neuroscience 2000). Each dot had a diameter of 0.3 degrees of visual angle, and the dot density was 0.44 dots per degrees square of visual angle. In the "eye-position" task, four stimulus positions and three fixation positions were used for a total of 12 conditions. Subjects maintaining fixation on one of three fixation spots, positioned either at the screen center or left or right of the screen center. Stimuli appeared randomly at one of four screen locations for a duration of 15 s. Stimuli were comprised of 48 randomly positioned dots moving coherently either upward or downward (direction chosen at random). After the stimulus had been presented at all four screen locations, the fixation mark was displaced to a new location and a new sequence of stimulus presentations began (after a 30-s blank interval to allow the BOLD signal to return to baseline). In each scan, all 12 conditions were presented once (D'Avossa et al. 2007). Subjects observed passively the stimuli while keeping fixation. Eye position was monitored with an infrared camera (60Hz).

3 healthy volunteers with normal vision participated in at least 6 sessions. Subjects lay on their backs and viewed binocularly stimuli displayed in a virtual reality sep-up (VisualStim XGA - Resonance Technology). The stimuli were generated in Matlab and displayed on a PC SVGA. BOLD responses were measured with a 1.5 T GE Signa Horizon system using a GRE-EPI sequence, sensitive to BOLD contrast (TR/TE/flip angle, 3000ms/50ms/90°; FOV=240 x 240 mm, matrix=64 x 64) while 3D high-resolution T1 structural images were obtained using a FSPGR sequence (TR/TE/TI/flip angle=12.4 ms/2.5 ms/700ms/10°; RBW=9.62 kHz; FOV= 240x240 mm; matrix=256X256). For each subject, a total of 14 scans were acquired for the motion localizing (116 functional volumes for each scan), 6 for the retinotopy (124 functional volumes) and 25 scans for the spatiotopic selectivity experiment (94 functional volumes). Brain Voyager QX (version 1.8, Brain Innovation) software package was used to analyze the BOLD response. All data were analyzed using an assumed heamodynamic response, obtained by convolving the duration of the stimulus with a standard impulse response function. To generate functional maps, we computed the intersection of different general linear model contrasts, maintaining at least the statistic threshold of $p<0.01$. We only labeled clusters of three or more contiguous voxels. For the spatiotopic experiment the response was computed as the modulation between the first 12s after and the 6s before stimulus presentation. Activity maps were superimposed on three-dimensional anatomical reference scans and normalized to the Talairach's space and flat maps, generated by segmenting and flatting the grey matter of the individual subject using the software Caret.

RESULTS

The retinotopy data in central fixation show that area MT complex (V5) has two distinct representation of the visual field: one sub-region shows predominantly contro-lateral visual field response (labeled as MT in Fig 1); the other, located more anteriorly, shows a stronger response to the ipsi-lateral than to contro-lateral stimuli (labeled MST in Fig 1). However this region has a clear differential response to stimuli along the vertical and horizontal meridian. The MT complex responds well to any type of flow. The foci with strongest response ($p< 0.00001$) to the different types of flow were only partially overlapping, the most consistent responses to a gradually changing flow being more extensive and more anterior than those to purely translational or rotational stimuli. The intersection between the various flow responses was found in the posterior and ascending limb of the inferior temporal sulcus (Figure 2). The intersection region is located in the border between LO2, MT and MST (green area of Figure 1). In this region, BOLD response to the ipsi- and contro-lateral stimuli measured for different gaze directions shows a clear effect of gaze, with the BOLD signals evoked by ipsi-lateral stimuli amplified when gaze is toward the contro-lateral hemi-space. This behavior is consistent with a responses coded in spatiotopic coordinate. The regions more posterior and more anterior to the intersection show a response only slightly modulated by gaze, demonstrating a primarily retinotopic selectivity. In conclusion, during passive observation, the region showing a spatiotopic selectivity (d'Avossa et al, NN 2007) is partially overlapping with the classical MT region and is strongly activated by all types of flow motion.

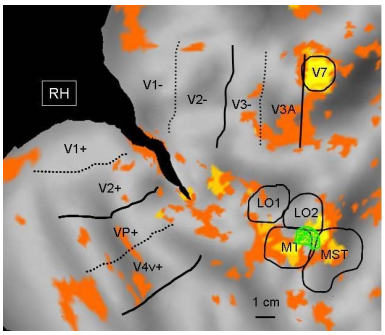

Figure 1: Flat map of one subject showing response to gradually changing flow ($p<0.02$). Dotted and continuous black lines indicate vertical and horizontal meridians respectively. Closed borders show regions of the lateral occipital sulcus and MT+ complex. MST region had a stronger response to ipsi-lateral than to contro-lateral motion.. In green is plotted the region intersection of all type of flow trajectory. This region shows also a spatiotopic selectivity.

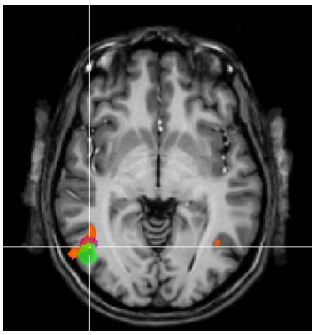

Figure 2: An example of a BOLD response map to flow motion, in the same subject of Figure 1 on one transverse slice (z=-1). The three colors represent the voxels that respond to three different kinds of motion (Orange: Spiral, Violet: Single Translation, Green: Inverting Translation).