## High-resolution fMRI of visual stimulation and attention in human superior colliculus

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**Introduction**. The superior colliculus (SC) is located on the dorsal surface of the primate midbrain. SC is a laminated structure: superficial layers receive inputs directly from the retina, intermediate layers show both visual and oculomotor responses, while deep layers exhibit multimodal responses. Previous work has demonstrated the presence of retinotopic maps of visual stimulation in monkey<sup>1</sup> and human<sup>2</sup> SC. Microstimulation of SC intermediate layers produces eye movements, and the movement maps are in good registration with those of visual stimulation<sup>3</sup>. The SC is also involved in the orientation of covert attention. Electrophysiology studies in monkeys have demonstrated that attention produces an enhancement in activity<sup>4</sup>, while microstimulation studies have shown a spatially specific enhancement of performance in visual tasks<sup>5</sup>. Here, we investigate the topography of visual attention in human SC.

Methods. Functional images were obtained on a 3T scanner using BOLD contrast, a spiral readout and 1.2-mm isometric voxels (17cm FOV, 8 slices, TE = 40 ms, TR = 1 s, 3 shots), and the product array coil. A double-oblique prescription covered the SC. Highresolution T1-weighted anatomical images were obtained on the same slice prescription to facilitate registration. Subjects (N=5) viewed images projected onto a panel in the scanner bore. To measure the retinotopy of visual stimulation, they viewed a 90°-wedge (2—10° eccentricity) of moving dots that rotated (24-s period) in a sequence of 30° steps around fixation. To control attention, subjects continually performed a speed-discrimination task within the wedge. In each session, subjects performed this task for 14—18 4-min runs. To measure the retinotopy of visual attention, subjects participated in 1—2 sessions where they viewed a full field of moving dots, while a small central cue oriented their attention to perform a similar discrimination task within a 90° wedge of the moving-dot field. The cue rotated in a similar fashion to the stimulation condition. To measure laminar profiles, we used similar moving-dot displays that either physically alternated between hemifields (1 session), or remained spatially constant while only the cue alternately directed attention between hemifields (2 sessions). Each run was compensated for motion and slow temporal trends. We then fit a sinusoid to the data to obtain complex amplitudes, which were then transformed to a reference volume (IR-prepared SPGR, 0.6-mm isometric voxels) obtained in a separate session that had been segmented to identify the superficial boundary of the midbrain. A smooth surface was fit to this boundary (Fig. 1), and a distance map from this surface provided a vector depth coordinate. Complex amplitude data was averaged in depth (0—1.8 mm) within the SC tissue to create phase maps that encode the spatial position of the stimulation and attention activity (Fig. 2). Laminar profiles (Fig. 3) were obtained from the hemifield-alternation data by resolving in depth the sinusoidal amplitudes averaged over 3-mm-diam regions upon the surface of the SC.

**Results**. We confirmed the presence of a retinotopic map of stimulation on the surface of the SC. The attention condition also produced retinotopic maps with similar orientations (Fig.2). For all subjects combined, correlation analysis showed detailed registration between the stimulation and attention maps both within individual colliculi (left:  $R^2 = 0.39$ ; right,  $R^2 = 0.44$ ) and for the colliculi together ( $R^2 = 0.90$ ); all correlations were highly significant (p = 0.0002) shift of 0.4 mm in between the profile centroids.

**Conclusions**. By using a novel combination of MRI methods, we obtained maps of stimulation and attention-driven activity in human SC with substantially better resolution than previously available, and measured variations in laminar activity profiles under experimental control. The data show that visual attention drives activity that is retinotopically and depth aligned with the superficial and intermediate layers of SC. Because these layers are associated with the mediation of visually guided eye movements, our data provide further support for an oculomotor basis for visual attention<sup>6</sup>.

<sup>1</sup>M. Cynader, N. Berman, *Journal of neurophysiology* **35**, 187 (1972). <sup>2</sup>K. A. Schneider, S. Kastner, *Journal of neurophysiology* **94**, 2491 (2005). <sup>3</sup>D. L. Sparks, *Physiol Rev* **66**, 118 (1986). <sup>4</sup>A. Ignashchenkova, *et al.*, *Nature neuroscience* **7**, 56 (2004). <sup>5</sup>J. R. Muller, *et al.*, *Proc Natl Acad Sci USA* **102**, 524 (2005). <sup>6</sup>T. Moore, *et al.*, *Neuron* **40**, 671 (2003).

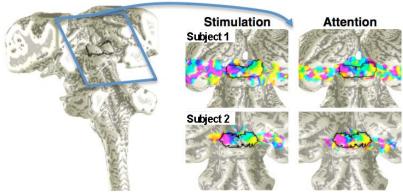


Figure 1: midbrain/brainstem surface

Figure 2: phase maps

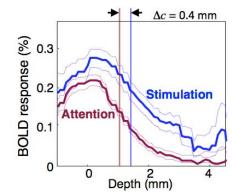


Figure 3: laminar profiles; dotted lines are 95% confidence