A Major Human White Matter Pathway Between Dorsal and Ventral Visual Cortex

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Abstract

Human visual cortex comprises many visual field maps organized into clusters. A standard organization separates visual maps into 2 distinct clusters within ventral and dorsal cortex. We combined fMRI, diffusion MRI, and fiber tractography to identify a major white matter pathway, the vertical occipital fasciculus (VOF), connecting maps within the dorsal and ventral visual cortex. We use a model-based method to assess the statistical evidence supporting several aspects of the VOF wiring pattern. There is strong evidence supporting the hypothesis that dorsal and ventral visual maps communicate through the VOF. The cortical projection zones of the VOF suggest that human ventral (hV4/VO-1) and dorsal (V3A/B) maps exchange substantial information. The VOF appears to be crucial for transmitting signals between regions that encode object properties including form, identity, and color and regions that map spatial information.

Key words: diffusion-weighted MRI, fiber tractography, vertical occipital fasciculus, visual cortex, white matter

Introduction

Over the last several decades, visual neuroscientists have learned how to use fMRI to identify multiple visual field maps (Fig. 1) in the living human brain (DeYoe et al. 1994; Engel et al. 1994, 1997; Sereno et al. 1995; Wandell et al. 2007; Silver and Kastner 2009; Wandell and Winawer 2011). Several theories have been proposed to characterize the organization of these visual field maps (Wandell et al. 2007). A key theory with substantial support distinguishes between maps located relatively dorsal and those located relatively ventral (Ungerleider and Mishkin 1982; Goodale and Milner 1992; Kravitz et al. 2013).

According to this theory, the ventral stream is mainly engaged in interpreting the properties of color, form, and objects. For example, several lateral and ventral visual field maps in humans (Fig. 1B) have clear stimulus selectivity, such as color selective response in hV4 (Zeki et al. 1991; McKeefry and Zeki 1997; Bartels and Zeki 2000; Wade et al. 2002, 2008; Winawer et al. 2010; Goddard et al. 2011) and shape selective responses in the lateral occipital (LO) areas (Malach et al. 1995; Grill-Spector et al. 2001; Larsson and Heeger 2006; Amano et al. 2009). The dorsal stream is engaged in interpreting spatial organization and guiding action, and dorsal maps in humans (Fig. 1A) have selectivity for motion and disparity (Tootell et al. 1997; Tsao et al. 2003; McKeefry et al. 2008) and spatial attention (Tootell et al. 1998; Schluppeck et al. 2005; Silver et al. 2005; Swisher et al. 2007; Silver and Kastner 2009).

Whereas responses to stimuli in the 2 streams differ (Ungerleider and Mishkin 1982; Goodale and Milner 1992), there are also examples showing relationships between responses measured in these 2 streams (Grill-Spector et al. 1998, 2000; James et al. 2002).
were collected at Stanford.

Diffusion-weighted magnetic resonance imaging (DWI) data

Subjects

MR Data Acquisition and Preprocessing

Materials and Methods

MR Data Acquisition and Preprocessing

Subjects

Diffusion-weighted magnetic resonance imaging (DWI) data were collected at Stanford’s Center for Cognitive and Neurobiological Imaging (http://cni.stanford.edu/). Five human subjects with normal or corrected-to-normal visual acuity participated in the study (5 males; age range 27–40, mean age 32.6 years old). All subjects participated in 1 scanning session to obtain a high-resolution T1-weighted anatomical volume, 1–3 functional MRI sessions to measure visual field maps, and 1 diffusion MRI session to measure high-spatial and high-angular resolution diffusion MRI (HARDI) data. Informed written consent was obtained from all subjects. The experimental procedures were approved by the Stanford University Institutional Review Board. The diffusion dataset was used in other publications (Pestilli et al. 2014; Rokem et al. 2015).

Diffusion Data

A dual-spin echo diffusion-weighted sequence (Reese et al. 2003) was used. In each scan, MR images were acquired for 96 different directions of diffusion weighting: The spatial resolution of the measurement was 1.5 x 1.5 x 1.5 mm. The b-value was set to 2000 s/mm² and TE was 96.8 ms. Ten nondiffusion-weighted images (b = 0) were acquired at the beginning of each scan. Two scans were performed.

MR images were motion corrected to the average b = 0 image in each scan, using a rigid body alignment algorithm, implemented in SPM (Friston and Ashburner 2004). The direction of the diffusion gradient in each diffusion-weighted volume was corrected using the rotation parameters from the motion correction procedure. Because of the relatively long duration between the RF excitation and image acquisition in the dual-spin echo sequence used, there is sufficient time for eddy currents to subside. Hence, eddy current correction was not applied. All preprocessing steps have been implemented in Matlab as part of the mrVista software distribution (https://github.com/vistalab/vistasoft).

For post hoc correction of EPI spatial distortion, measurements of the B₀ magnetic field were performed to DWI data. Field maps were collected in the same slices as the functional data using a 16-shot, gradient echo spiral trajectory pulse sequence. Two volumes were successively acquired, one with TE set to 9.091 ms and one with TE increased by 2.272 ms, and the phase difference between the volumes was used as an estimate of the magnetic field. To track slow drifts in the magnetic field (e.g., due to gradient heating), field maps were collected before and after the diffusion runs as well as periodically between diffusion runs.

Anatomical MRI Acquisition and Tissue Segmentation

The white and gray matter border was defined using a T₁-weighted FSPGR image (0.7 x 0.7 x 0.7 mm in 4 subjects and 1 x 1 x 1 mm in 1 subject). White/gray matter tissue contrast was increased by averaging 4 T₁ measurements acquired in the same scan session. An initial segmentation was performed using an automated procedure in Freesurfer (Fischl 2012) and refined manually (Yushkevich et al. 2006) (http://www.itksnap.org/pmwiki/pmwiki.php).

Functional Data and Visual Field Maps Estimation

The visual field maps in each hemisphere were identified using the population receptive field (pRF) modeling for fMRI data (Dumoulin and Wandell 2008). Subjects participated in at least 4 fMRI scans (TR: 1.5 s; voxel size; 2.5 mm isotropic in 4 subjects and 2.5 x 2.5 x 3 mm in 1 subject). Stimulus design and analysis methods were the same as the bar scans used in previous studies (Dumoulin and Wandell 2008; Amano et al. 2009; Winawer et al. 2010).

Retinotopic maps were created by projecting the pRF estimates onto cortical surfaces. The borders between most visual areas (V1, V2, V3, V3A/B, hV4, VO-1, VO-2, LO-1, and LO-2) were marked manually at the reversals in polar angles. The borders between hV4 and VO-1 are determined by an eccentricity reversal (Brewer et al. 2005) and an anatomical landmark (Wittfoht et al. 2014). VO-2 was not identified in 2 of 10 hemispheres. Maps V3A and V3B were combined in the main analyses, because we could identify the boundary between these maps in only 8 of 10 hemispheres. We performed 1 additional analysis separating V3A and V3B in these 8 hemispheres.

Selection and Validation of White matter Connectomes

We used probabilistic tractography to generate candidate connectome of the human occipital lobe (Tournier et al. 2012). We
used Linear Fascicle Evaluation (LiFE; Pestilli et al. 2014) to optimize these connectomes by eliminating false alarm fascicles and establish the strength of evidence for specific tracts. The LiFE software is available at: http://francopestilli.github.io/life.

Candidate Connectomes Generation
Fiber tracking was performed using MRtrix (Tournier et al. 2012). Diffusion-weighted images were motion-compensated and aligned to the high-resolution T1-weighted anatomical image. Half of the diffusion data was used for fiber tractography, and the other half was used for cross-validation (see below).

The white matter volume was used as seed region for fiber tracking. The white matter of the occipital lobe was identified from the tissue-type segmentation (see above) and resampled at the resolution of the diffusion data. We used constrained spherical deconvolution (CSD; Tournier et al. 2007) and probabilistic tractography (step size: 0.2 mm; maximum length: 200 mm; minimum length: 10 mm; FOD amplitude cutoff: 0.1) to generate stochastic tractography (step size: 0.2 mm; maximum length: 200 mm; minimum length: 10 mm; FOD amplitude cutoff: 0.1) to generate a large inhomogeneous fiber bundle containing more than the VOF. The core of the VOF was identified by eliminating fibers classified as outliers for direction, length, and position. To do so, we 1) calculated each fiber’s direction in the white matter portion between 2 waypoint ROIs and removed fibers whose direction deviated more than 2 SD from the mean VOF direction, 2) removed fibers with a length >3 SD above mean VOF fiber length, and 3) removed fibers with position >3 SD away from the mean position of the VOF (Yeatman, Dougherty, Myall et al. 2012). The second and third steps were repeated recursively 3 times. Visualization of the tracts was performed using the Matlab Brain Anatomy toolbox (https://github.com/francopestilli/mba).

Cortical Projection of the VOF
We combined the functionally defined cortical visual field map with the VOF terminations to identify the cortical projection zones of the VOF and their relation to the visual field representations. To identify the cortical projection zones of the VOF, we collected the X, Y, and Z coordinates of the termination of all the VOF fibers. We extended these terminations into the cortical gray matter by applying a 3-dimensional Gaussian smoothing and summing the X, Y, and Z coordinates of fibers terminating within the same cortical voxel. We repeated this process 3 times by using 3 different optimized connectomes (see above) and then averaged. We plotted the normalized projection density on the smoothed cortical surface (see Figs 3A and 4A).

We also measured the coverage of VOF projection at each visual field map. The coverage is defined as the proportion of gray matter voxels in each map within a close distance to the VOF terminations. The coverage is computed 3 times, with different optimized connectomes in each hemisphere, and the results were then averaged. We further repeated this procedure by utilizing 3 distances (1.5, 3, or 4.5 mm in volumetric space) to relate the VOF terminations and the cortical ROIs. We considered distances up to several millimeter to allow for small errors in mapping the
locations of the ROI boundaries and fiber terminations, the latter of which may be subject to small systematic biases such as a tendency to terminate in sulci rather than gyri (Fig. 4A). Figures 3B and 4B describe the proportion of each map covered by the VOF. Results are averaged across all 10 hemispheres.

We compared the VOF projection across optimized connectomes generated using different parameters within optimal range ($l_{\text{max}} = 4, 6, 8, \text{ and } 10$; the minimum radius of curvature $= 0.5$ and $1 \text{ mm}$). We utilized $3 \text{ mm}$ distance to define a cortical projection of VOF in each optimized connectome. Supplementary Figures 7, 8, 13, and 14 describe the comparison of VOF coverage across different connectome models.

**Results**

The existence of the VOF was established by classical and recent post-mortem fiber dissection studies (Martino and Garcia-Porrero 2013; see Yeatman, Weiner et al. 2014 for a review on classical studies). But the relationship between the VOF cortical projection zones and early visual field maps was unknown. Here, we used diffusion MRI and fiber tractography to identify the posterior portion of the VOF in 10 hemispheres (see Supplementary Materials and Methods). We then assessed the strength of the statistical evidence supporting the existence of the VOF given the measured diffusion signal (Pestilli et al. 2014). Finally, we used fMRI to characterize the VOF cortical projections with respect to the dorsal and ventral visual field maps.

**VOF Identification and Statistical Evaluation**

Figure 2A shows the VOF identified in 1 representative hemisphere (see Supplementary Materials and Methods, and Supplementary Fig. 2). The VOF projects to both the dorsal part of occipital cortex and the lateral portion of ventral occipital cortex. The VOF is located posterior to the arcuate fasciculus (Martino and Garcia-Porrero 2013) and lateral to the optic radiation (Fig. 2A). We identified the VOF in 10 hemispheres (Fig. 2B) in a consistent position relative to the posterior segment of the arcuate fasciculus and the optic radiation. The mean VOF length is $3.7 \text{ cm} (SD = 0.3 \text{ cm}, N = 10)$ and its volume is $2.3 \text{ mL} (SD = 0.5 \text{ mL}, N = 10)$. The range of sizes is similar to that observed in the surface area of visual field maps (Dougherty et al. 2003). The VOF location can be inferred from the PDD map generated by a diffusion tensor fit (Pajevic and Pierpaoli 1999; Wakana et al. 2004; Yeatman et al. 2013). Supplementary Figure 3 shows the location of the posterior portion of the VOF identified using tractography (Tournier et al. 2012; Pestilli et al. 2014) and projected on the PDD map of representative brain slices. The VOF location is blue, indicating a primarily vertical (superior–inferior) PDD. Supplementary Figure 4 also shows the location of VOF identified from a PDD map in Human Connectome Project dataset (Van Essen et al. 2013).

We used the LiFE algorithm (Pestilli et al. 2014; see Supplementary Materials and Methods and Supplementary Fig. 2) to establish the strength of evidence in favor of the VOF. The LiFE algorithm treats a connectome (the complete set of white matter tracts and connections in a brain volume; Sporns et al. 2005; Hagmann et al. 2010) as a model of the measured diffusion signal. LiFE uses the connectome model to generate synthetic diffusion signals. While generating synthetic diffusion signal, LiFE eliminates fascicles that do not contribute to the diffusion prediction (false alarm fascicles; Pestilli et al. 2014). The RMSE between the synthetic and the measured signal measures the accuracy of the connectome model. The connectome without false alarm fascicles is called the optimized connectome.

We used LiFE to compute the accuracy of several optimized connectome models; each was constructed using different tractography (minimum radius of curvature; Tournier et al. 2012) and constrained spherical deconvolution parameters ($l_{\text{max}}$; see Supplementary Materials and Methods; Tournier et al. 2007, 2012). The accuracy of the optimized connectome derived using the recommended parameters ($l_{\text{max}} = 8$; minimum radius of curvature $= 1 \text{ mm}$; Tournier et al. 2012) was equal or better than other choices (see Supplementary Figs 5 and 6; also Supplemental Materials and Methods). All subsequent analyses were performed using the recommended parameters.

Finally, we used LiFE to evaluate the strength of evidence (S; Pestilli et al. 2014) supporting the existence of the VOF. S is computed by removing the VOF from the optimized connectome and recalculating the prediction error (see Virtual lesion in Supplementary Materials and Methods). The mean strength of evidence is $S = 28.89 (28.98, 29.80, 41.33, 27.55, \text{ and } 19.68 \text{ for left hemispheres}; 29.91, 32.81, 31.85, 30.11, \text{ and } 16.90 \text{ for right hemispheres}).$ Supplementary Figure 9 shows the comparison of the $S$ on the VOF and other major fascicles reported in a previous study (Pestilli et al. 2014). The evidence on the VOF is smaller than several major fascicles (SLF, ILF, and Arcuate) but comparable with relatively smaller fascicles (e.g., Uncinate). Hence, there is visible evidence (see Supplementary Figs 3 and 4) and very strong statistical evidence supporting the existence of the VOF in the human brain.

**Dorsal VOF Projections**

Next, we established the dorsal and ventral visual field maps containing the VOF cortical projections. The visual field map boundaries and pRFs were measured using fMRI (see Supplementary Materials and Methods; Dumoulin and Wandell 2008). Figure 3A shows the cortical projection areas of the posterior portion of the VOF on the dorsal cortical surface of 2 hemispheres.

Figure 3B describes the proportion of the voxels in each map that are within a specific distance ($1.5, 3, \text{ and } 4.5 \text{ mm}$) of a dorsal VOF termination. There is a major dorsal VOF projection to V3A/B. Across all hemispheres, the majority of VOF terminations are within $4 \text{ mm}$ of V3A/B. We frequently observe projections to neighboring V3d as well. Across 10 hemispheres, $82.0\%$ of these posterior VOF dorsal cortical projections terminate near V3A/B or V3d, but they are rarely near V2d, V1, or the intraparietal sulcus (IPS) maps. The anterior portion of the VOF contains additional projection zones in more anterior dorsal and ventral cortex. These results are robust to the choice of diffusion model and tractography parameters (see Supplementary Figs 7 and 8).

**Strong Evidence Supporting VOF Projections to V3A/B**

To test the strength of the evidence supporting the VOF projections to V3A/B, we compared the connectome prediction error with the VOF fascicles projecting to V3A/B removed (lesioned connectome) or not (unlesioned connectome). The prediction error is substantially higher when these fascicles are removed. The mean strength of the evidence ($S$) for the VOF projections to V3A/B is $25.72$ (see Supplementary Fig. 10).

We repeated the analysis for V3d and V2d. Evidence for VOF projections for V3d is lower, $S = 15.34$ and is small for V2d (mean $S = 6.53$; see Supplementary Fig. 10). The data strongly indicate that the VOF projects to V3A/B and demonstrates a considerable statistical evidence for projections to V3d.:

1. **Figure 3A** shows the cortical projection areas of the posterior portion of the VOF on the dorsal cortical surface of 2 hemispheres.
2. **Figure 3B** describes the proportion of the voxels in each map that are within a specific distance of the VOF.
3. **Figure 3C** illustrates the strong evidence supporting the VOF projections.
4. **Figure 3D** demonstrates the weak evidence for projections to V3d.

These results highlight the critical role of the VOF in the human brain, supporting its importance in visual processing.
support the VOF projections to V3A/B. There is some evidence for the VOF projections to V3d and smaller evidence for V2d.

**Dorsal VOF Projections Are Uniformly Distributed Between V3A and V3B**

We managed to subdivide maps V3A and V3B in 8 out of 10 hemispheres. The VOF projects to large portions of both V3A and V3B (see Supplementary Fig. 11). The strength of the evidence is comparable for V3A and V3B (see Supplementary Fig. 12; V3A, mean $S = 23.40$; V3B, mean $S = 21.29$), suggesting that VOF projections are present in both V3A and V3B.

**Ventral VOF Projections**

We analyzed the VOF cortical projection areas in relation to visual field maps in the posterior occipital ventral stream (Fig. 4A). There are VOF projections to hV4 in all 10 hemispheres, so that the majority of hV4 voxels are within 4 mm of VOF terminations (Fig. 4B). There are limited projections to V3v, mostly restricted to the lateral portion of the map, representing foveal visual field (Fig. 4A). Very few fascicles project to V2v. The VOF also terminates near other ventral maps such as VO-1 (Brewer et al. 2005), and lateral maps such as LO-1 and LO-2 (Larsson and Heeger 2006; Amano et al. 2009; Silson et al. 2013). However, the map...
coverage in these regions is much lower than the hV4 map coverage (Fig. 4B). The results are consistent across a range of diffusion model and tractography parameters (see Supplementary Figs 13 and 14).

In addition, the VOF has large projections into cortical regions with difficult visual field maps assignment due to their predominantly foveal representation and to the existence of MRI artifacts (No Man’s Land; Winawer et al. 2010). These projections are likely to include the pRFIT region (Kolster et al. 2010) and one of the face selective patches (IOG-faces; Weiner and Grill-Spector 2010). The ventral VOF projections are also likely to extend to regions anterior to VO-1 including the visual word form area (VWFA; Cohen et al. 2000, 2002; Ben-Shachar et al. 2007; Yeatman et al. 2013).

Strength of Evidence Supporting VOF Projections into hV4
To test the strength of the evidence supporting VOF projections to hV4, we compared the connectome prediction error with and without the VOF fascicles projecting to hV4 (virtual lesion). There is reliable evidence for VOF projections to hV4 (S = 16.68; see Supplementary Fig. 15) and some evidence for VO-1 (S = 11.58; see Supplementary Fig. 15). The strength of evidence for VOF projections to V3v, LO-1, and LO-2 is smaller than for hV4 (S = 9.59, 8.47, and 9.18, respectively; see Supplementary Fig. 15). The strength of evidence is small for V2v (S = 5.04; see Supplementary Fig. 15). The analyses support a projection pattern in which the principal VOF terminations are near hV4 and perhaps VO-1.

Stronger Evidence for VOF Projection to Ventro-lateral Than Ventro-medial Cortex
Early visual areas, such as V1, V2, and V3, are located on the medial surface of the occipital lobe. The analysis of the ventral VOF projections suggests that ventral maps on medial surface (V2v and V3v) do not receive major VOF projections (Fig. 4). The visual field maps located on the lateral side instead (hV4, VO-1, and LO-map) receive larger VOF projections.

To test whether the VOF projects primarily to ventro-lateral cortex, we identified the anatomical location of the collateral
invariance in object recognition. Complementing these findings, there are studies showing object-selective responses in dorsal regions (Grill-Spector et al. 2000; James et al. 2002; Fang and He 2005; Konen and Kastner 2008; Vinberg and Grill-Spector 2008).

Rokers and colleagues (2009) reported that in addition to hMT+ and V3A, LO also showed selectivity for 3-dimensional motion. Costagli and colleagues (2014) measured the cortical response to increments and decrements of motion coherence, and identified that V3B and hV4 similarly showed positive responses to both increments and decrements. Other lines of studies (Dövençoğlu et al. 2013; Murphy et al. 2013) demonstrated that V3B is involved in stereo cue integration (disparity, texture, and shade), which could be the outcome of dorsal-ventral communication. A recent study (Sabers et al. 2015) showed that saccade planning evokes BOLD activity not only in dorsal (V3A/B, IPS0) but also in ventral visual areas (hV4, VO-1). All of these studies suggest substantial communication between the dorsal and ventral maps. The anatomical description of the VOF makes it the likely pathway to carry signals coordinating dorsal and ventral stream processing.

Comparison Between Human and Macaque

There are many functional and structural differences between visual cortex in human and macaque. For example, concerning the visual field maps, interspecies differences have been identified in the position of V4 (McKeefry and Zeki 1997; Wade et al. 2008; Arcaro et al. 2009; Winawer et al. 2010; Goddard et al. 2011; Witthoft et al. 2014), the volume of V3 (Brewer et al. 2002; Dougherty et al. 2003; Lyon and Connolly 2012), and responses to moving stimuli in V3A (Tootell et al. 1997; Vanduffel et al. 2001). Moreover, there are no certain homologies between the human V3B (Smith et al. 1998; Press et al. 2001) and the LO-maps (Larsson and Heeger 2006; Amano et al. 2009) and macaque maps. All of these maps have been identified as VOF terminations in this study.

Given these significant interspecies differences, it is important to understand white matter tracts and their cortical projections in humans directly. Identifying the path of the white matter tracts in humans has the added advantage that properties of the tracts can be studied in relation to health, disease, and development (Dougherty et al. 2007; Fields 2008; Thomas et al. 2009; Thiebaut de Schotten et al. 2011; Thomason and Thompson 2011; Lebel et al. 2012; Wandell et al. 2012; Yeatman, Dougherty, Ben-Shachar et al. 2012; Johnson et al. 2013; Wandell and Yeatman 2013; Ogawa et al. 2014; Tavor et al. 2014; Yeatman, Wandell et al. 2014; Allen et al. 2015; Gomez et al. 2015).

The present study extends post-mortem macaque brain studies (Felleman and Van Essen 1991; Ungerleider et al. 2008) to in vivo methods in the human brain. We have learned that the VOF is a major tract occupying a substantial volume of the occipital white matter. We show that its path and projections can be reliably defined using modern diffusion MRI methods in living brains. This is the first study to characterize the cortical projections of the VOF in relation to the visual field maps.

Early Hubs of Ventro-Dorsal Visual Communication

Primate V2 and V3 have split representations of the contralateral hemifield, with dorsal and ventral regions responding to stimuli in the lower and upper quarterfields, respectively. In humans, the visual field maps adjacent and anterior to V3 are not split: these maps have a full hemifield representation confined within the dorsal (V3A/B) and ventral (hV4 and VO-1) surfaces (Tootell

Figure 5. The VOF communication diagram. Schematic diagram of the VOF projections. Visual field topography was described in a flattened format for the right hemisphere (Larsson and Heeger 2006). Gray regions depict the projection zone of VOF (light gray, dorsal; dark gray, ventral).
et al. 1997; Press et al. 2001; Brewer et al. 2005; Arcaro et al. 2009; Winawer et al. 2010; Goddard et al. 2011; Wandell and Winawer 2011). Because of their hemifield representation, these maps are natural candidates for information hubs that communicate between ventral and dorsal streams. We have shown that the VOF communicates preferentially between these maps. Future measurements and models will benefit from mapping the functional responses of these maps in humans and by considering their potential role as communication hubs between dorsal and ventral cortex.

Conclusion

Many cognitive activities such as reading this page require fast and accurate coordination between motor actions (e.g., eye movements) and object identification (e.g., word recognition; Vidyasagar and Pammmer 2010). The human brain comprises distinct cortical regions specialized for seeing objects and processing spatial information that are separated by several centimeters in ventral and dorsal occipital cortex. The anatomy of the human brain requires a major white matter communication pathway between the dorsal and ventral streams. The VOF is a strong candidate for channeling communication between dorsal and ventral visual streams. Characterizing the VOF in individual, living human brains provides a new opportunity for understanding how signals pass between dorsal and ventral visual cortex and to understand the role of these signals in health and disease.

Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/.

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Notes

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