

Polar-angle representation of saccadic eye movements in human superior colliculus

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ABSTRACT

The superior colliculus (SC) is a layered midbrain structure involved in directing both head and eye movements and coordinating visual attention. Although a retinotopic organization for the mediation of saccadic eye-movements has been shown in monkey SC, in human SC the topography of saccades has not been confirmed. Here, a novel experimental paradigm was performed by five participants (one female) while high-resolution (1.2-mm) functional magnetic resonance imaging was used to measure activity evoked by saccadic eye movements within human SC. Results provide three critical observations about the topography of the SC: (1) saccades along the superior-inferior visual axis are mapped across the medial-lateral anatomy of the SC; (2) the saccadic eye-movement representation is in register with the retinotopic organization of visual stimulation; and (3) activity evoked by saccades occurs deeper within SC than that evoked by visual stimulation. These approaches lay the foundation for studying the organization of human subcortical – and enhanced cortical mapping – of eye-movement mechanisms.

Introduction

The superior colliculus (SC) is a layered midbrain nucleus with multiple functions including processing vision, orienting attention, priming head movements, generating saccadic eye movements and integrating multiple sensory inputs. The SC is organized into seven laminae of distinct cytoarchitecture with alternating cellular and fiber character. There are three superficial layers and four inner layers (Wurtz and Albano, 1980). The superficial layers receive direct retinal input and contain visual neurons with retinotopically organized receptive fields (Cynader and Berman, 1972; Feldon and Kruger, 1970). The inner layers are separated into intermediate and deep layers. The two intermediate layers contain motor output neurons that control eye movements (Robinson, 1972), whereas the two deep layers contain multisensory integration neurons (Meredith and Stein, 1990; Sprague and Meikle, 1965).

The oculomotor function of the SC was first discovered by electrical stimulation (Adamuk, 1872; Donders, 1872), and later induced via strychnine (Apter, 1946) in anesthetized cats. Extensive studies in alert monkeys via electrical stimulation (Robinson, 1972), neuronal recordings (Mohler and Wurtz, 1976), and lesions (Wurtz and Goldberg,

1972) then characterized the non-human primate topography of the SC [see several reviews (Fuchs et al., 1985; Sparks and Hartwich-Young, 1989; Sparks and Jay, 1986; Wurtz and Albano, 1980)]. The intermediate layers of monkey SC contain a retinotopically organized saccadic eye-movement map (Schiller and Stryker, 1972). Saccade magnitude is roughly mapped along the rostral-caudal axis of monkey SC, whereas saccade direction is mapped along the medial-lateral axis of the SC. The mapping is not linear, with over-representation of small-magnitude saccades, and of polar angles close to the horizontal meridian (Sparks et al., 1976). Also, the SC topography shows a small but variable amount of tilt in the left-right direction that is in rough correspondence to the anatomic tilt of the colliculi relative to the neuraxis (Robinson, 1972). Recent studies have further revealed that the upper visual field is over-represented, comprised of smaller and more sensitive receptive fields (Hafed and Chen, 2016).

In humans, studies to infer SC function have historically been restricted to whole-brain functional magnetic resonance imaging (fMRI). Whole-brain or low-resolution (i.e., ≥ 2 -mm voxels) fMRI has documented saccade-related activity in SC (de Weijer et al., 2010; Furlan et al., 2015; Krebs et al., 2010), and reach-related functions performed by

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the deep layers of SC (Himmelbach et al., 2013). However, the low-resolution measurements did not delineate the detailed topography of SC functions. Further, previous human studies of saccadic mapping in cortex, not SC, have attempted to use fMRI phase-encoding approaches (Connolly et al., 2015; Konen and Kastner, 2008; Schluppeck et al., 2005; Sereno et al., 2001) but with two critical limitations: (1) a very low duty cycle and (2) reverse saccades made immediately after forward saccades. The low duty cycle forces participants to fixate most of the time instead of performing saccades, which reduces the evoked hemodynamic activity. A paradigm with a higher duty cycle that isolates saccades in one direction is likely to be crucial to getting reliable SC topography measurements with fMRI.

More recent human fMRI studies were able to demonstrate the presence of visual stimulation retinotopy (Schneider and Kastner, 2005), and covert attention signals (Schneider and Kastner, 2009) in superficial SC using higher resolution fMRI ($1.5 \times 1.5 \times 2$ -mm voxels) targeted specifically to midbrain. Our laboratory expanded upon these studies using higher resolution fMRI (1.2-mm cubic voxels) to demonstrate a detailed transverse retinotopic organization of visual attention and stimulation upon SC (Katyal et al., 2012, 2010; Katyal and Ress, 2014).

Here, we improved those methods and developed a novel task to measure the polar angle representation of saccadic eye movements, elucidating their topography within human SC. Using our previous visual stimulation paradigm optimized for human fMRI in SC (Katyal et al., 2010), we show that these eye movement maps are in register with the retinotopy observed in SC superficial layers. Finally, we demonstrate that the measured activity is elicited from the intermediate layers. Altogether, our results again confirm macaque electrophysiology, and create an experimental framework for further experiments in human eye-movement physiology both in brainstem and cortex.

Materials and methods

Participants

We recruited five participants (4 males, all right-handed) to undergo several ~2 h long scanning sessions. One-to-two sessions were acquired for each participant to discern the polar-angle representation of leftward and rightward saccadic eye movements separately, which were expected to evoke activity primarily in the contralateral SC. Each eye-movement session consisted of 12–16 278-s runs. One-to-two scanning sessions were also acquired from each participant for visual stimulation retinotopic mapping. Visual stimulation experiments were intended to evoke

activity in both SC since the entire visual field was stimulated in a single session. Retinotopy sessions consisted of 14–16 228-s runs. Participants gave informed consent prior to scanning based on our approved protocol from the Baylor College of Medicine Institutional Review Board.

Experimental design

Stimuli were generated using MATLAB R2015a (Mathworks, Natick, MA) and PsychToolbox-3 (Brainard, 1997). Stimuli were presented on a 32" LCD BOLD Screen (Cambridge Research Systems, Kent, UK) at the back of the scanner bore 1.3 m away from the participants' eyes. The display was gamma corrected using an i1 Pro 2 spectrophotometer (X-Rite, Grand Rapids, MI), and had a mean luminance of 305 cd/m².

We designed a paradigm in which participants performed many saccades in one direction while minimizing saccades in the opposing direction (see **Movie M1**). Participants made saccades either to the left or to the right (activating primarily the contralateral SC) while we cyclically varied the vertical component of the saccade to correspond to the lower, horizontal, and upper visual field (Fig. 1). Participants performed three 6° saccades guided by a green dot target in a static grid of 12 red dots. The static red dots were arranged as 4 dots separated by 6° along each of the three principle axes (horizontal, 45° diagonal, and -45° diagonal). The use of a static grid reduced differential contrast effects from retinal slip. Although each saccade and subsequent pursuit produces motional stimulation, the shape of the static grid minimizes differential effects of this stimulation between angular conditions. The use of green-red color contrast minimized the effects of bottom-up color contrast in target discrimination. Further, human SC has recently been shown to adapt to red-green contrast (Chang et al., 2016), so our static red-green grid reduces cue-evoked visual stimulation during saccadic eye movement measurements.

Supplementary video related to this article can be found at <https://doi.org/10.1016/j.neuroimage.2017.12.080>.

Participants initially held fixation at an upper corner of the display. The first saccade was initiated when an adjacent red dot turned green to indicate the saccade target. Once the saccade was made, participants had to discriminate between the outlines of two possible shapes (circle or square) presented within the target dot. This required visual attention to be engaged and saccades to be made more reliably. Participants responded via button press, which triggered the green dot to appear at the next target along the current axis. After three saccades, the participants then performed a smooth pursuit (1.2 s) back to the first dot. Saccades and the pursuit were continued along the same axis for 9.6 s,

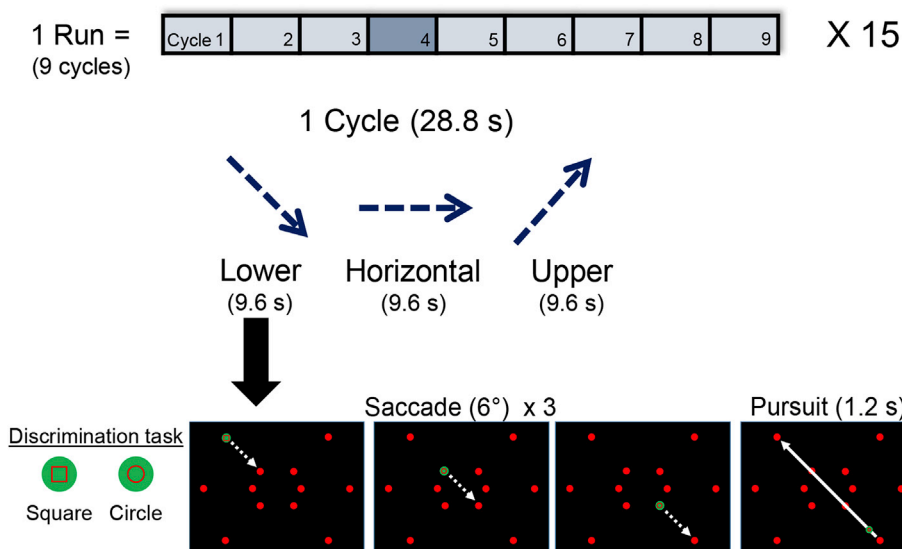


Fig. 1. Participants performed visually-guided saccades to measure the polar-angle representation of saccades in SC. In each session, activity from one SC was measured by having participants perform saccades toward a single hemifield (right shown here) along a particular polar angle. The stimulus screen showed a static grid of 12 red dots with one target dot turned green to indicate the saccade target. Participants made three 6° saccades along the current polar angle, after which a 1.2-s visually-guided smooth pursuit was made back to the origin along that axis. Upon fixation onto target dots and during the smooth pursuit, participants performed an object discrimination task (square or circle) to keep attention engaged and improve the reliability of eye movements. In each 28.8-s cycle, the vertical component of the saccades progressed through three polar angles: -45° (lower), 0° (horizontal), and +45° (upper). Each session consisted of 15–4.5-min runs, each of which included 9 cycles. (See Fig. S1 for evolution of task design).

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