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Role of the calcarine cortex (V1) in perception of visual cues for saccades

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Abstract

Objective: To determine the initial level at which the pathways for cue perception, saccades and antisaccades diverge.
Methods: Two procedures: single pulse transcranial magnetic stimulation (sTMS) over posterior occiput and backward masking were used. A visual cue directed saccades to the left or right, either a pro-saccade (to the side of the cue but beyond it) or an antisaccade, i.e., contraversive saccade. No visual target was presented.
Results: Latencies of the two types of saccades did not differ. Focal sTMS applied unilaterally over V1 suppressed both perception of a cue flashed 80–90 ms earlier contralaterally (but not ipsilaterally) and the appropriate saccade. Masking at a delay of 100 ms abolished the appropriate saccade and cue perception.
Conclusions: V1 is essential for the perception of a flashed cue and for executing appropriate pro- and contraversive saccades. Masking may occur beyond V1, where the pathways for perception and for saccades at least to the next visual processing level start separating.
Significance: VI is needed for rapid, accurate perceptual and motor responses to the crudest (left versus right) cues. It is unlikely that the "where" system can have a major direct input bypassing V1.

Keywords: TMS; Visual cortex; V1; Pro-saccades; Contraversive saccades; Masking

1. Introduction

A remarkable feature of vision in a conscious human is the ability to guide movements, e.g., of a finger or the eyes, swiftly and accurately towards a suddenly appearing object in the external world. Similarly, prompted by a visual cue, a subject can voluntarily switch the gaze as instructed to any site in the visual field without alighting on the site of the cue. Do such movements depend on processing of visual information by V1 and what is their relationship to conscious perception of the cue? Clearly, some visually guided behavior by conscious patients is spared after a V1 lesion; stimuli presented in the blind hemifield can be localized by pointing or by eye movement (Poeppel et al., 1973; Weiskrantz et al., 1974; Perenin and Jeannerod, 1975; Zihl, 1980; Weiskrantz et al., 1995; Stoerig and Cowey, 1997). However, evidence is lacking in these patients that the desired movements can occur with the brevity of delay and accuracy of execution attainable in a normal subject. Nevertheless, a visual reaction time paradigm can bypass V1. The expiratory response in making a "ugh" sound to a flashed visual stimulus can result from activation of the external oblique muscle so early as to

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make unlikely that stimulus evoked activity in V1 and the motor cortex mediated the response (Amassian et al., 1995).

In this study, first we used focal TMS over the calcarine cortex of one side to suppress processing of the visual cue in the contralateral hemifield. The objective was to determine if the pathways for saccades and perception of the visual cue were separate or proximate at this level. For example, the processing of the cue for the appropriate saccade might bypass V1 and utilize a subcortical relay in the superior colliculus, leading to its correct localization to either side. Given that a cued antisaccade (i.e., contraversive saccade) would require an opposite vector for its execution, the effect of unilateral calcarine suppression was also investigated. Second, to study the later processing levels, we used backward masking (Michaels and Turvey, 1979) to suppress the cue at a mask delay of 100 ms or more, because the suppression is then thought to occur beyond V1 (Amassian et al., 1993a,b). A preliminary account of these findings was published (Lalli et al., 2000).

2. Methods

2.1. Subjects

Ten subjects (six males and four females) participated in the comparison of saccade and antisaccade latencies (Fig. 1); of these, four were naïve and six were involved over a long term and understood the hypothesis being tested. From among the 10 subjects, for the TMS studies (Fig. 2), three were naïve and the fourth had experienced TMS outside the occipital area. In the masking studies (Figs. 3 and 4), seven subjects were tested of which six were naïve. Their ages ranged from 16 to 65 years (32 ± 16.7; mean, SD). None had a previous history of eye movement disorder, epilepsy or other neurological diseases. The Institutional Review Board approved the use of sTMS and written consent was obtained from the subjects.

2.2. Recording of eye movements

In the TMS experiments, eye movements were recorded using an infrared camera (ISCAN, Inc., Burlington, MA) at 120 Hz sampling rate. The subjects were seated and the chin and head were in a "GAMBS" ophthalmological support frame. For calibration, subjects executed saccades to predetermined locations 5°, 10°, 15°, 20°, 30°, and 40° from the fixation point. The analog output of the ISCAN was displayed on a digital oscilloscope. In the masking experiments, eye movements were recorded with metal electrodes placed at the external canthi. The ground electrode was placed on the middle of the forehead. The electro-oculogram (EOG) was amplified and displayed on a digital oscilloscope. RC coupling rather than DC coupling was used, with a low frequency response down to 0.2 Hz because it improved the stability of the recording without distortion of the onset latency.

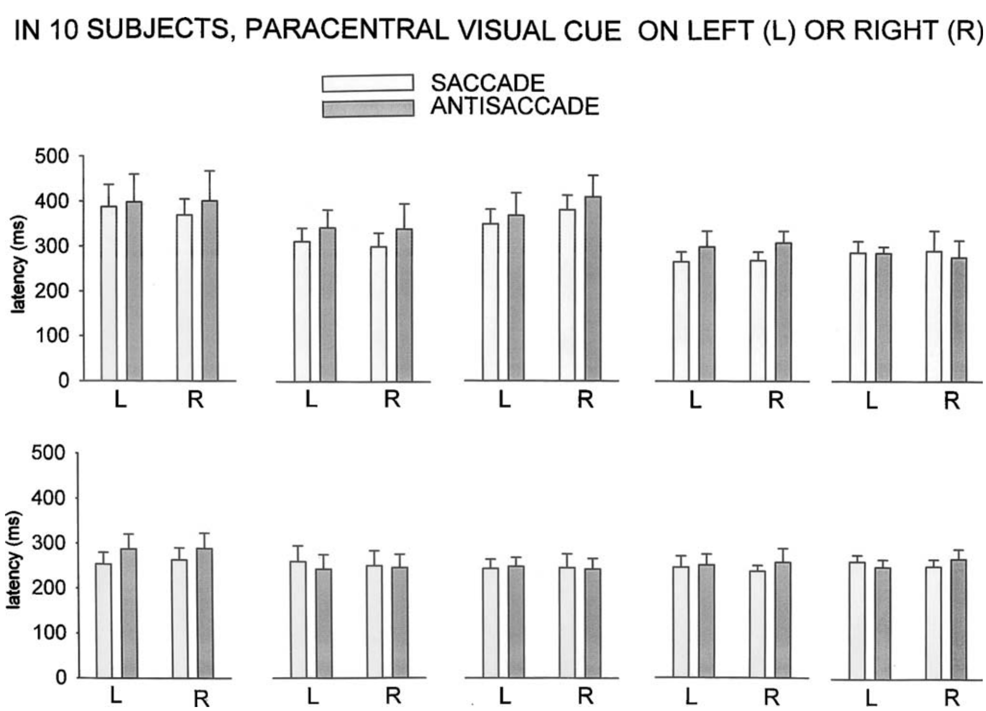

Fig. 1. Latencies of saccades and antisaccades to cues in 10 subjects. The mean latencies and SD of saccades (open columns) and antisaccades (gray columns) are shown with the cue presented in the left or right visual field. In each of six subjects, 20 or more (leftward and rightward, interspersed) saccades and similar numbers of antisaccades were charted; the remaining four subjects were repeatedly studied in two to four sessions and averaged for each subject. Although antisaccade latencies in 14 of 20 comparisons slightly exceed those of saccades, the difference was not significantly different (t test $p > 0.05$). In the other six comparisons, antisaccade latencies were briefer.