

Effects of electrical microstimulation in monkey frontal eye field on saccades to remembered targets

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Abstract

Spatially selective delay activity in the frontal eye field (FEF) is hypothesized to be part of a mechanism for the transformation of visual signals into instructions for voluntary movements. To understand the linkage between FEF activity and eye movement planning, we recorded neuronal responses of FEF neurons while monkeys performed a memory-saccade task. We then electrically stimulated the same sites during the memory-delay epoch of the task. The stimulation currents used were subthreshold for evoking saccades during a gap-fixation task. Microstimulation resulted in changes in the spatial and temporal components of saccade parameters: an increase in latency, and a shift in amplitude and direction. We performed a vector analysis to determine the relative influence of the visual cue and electrical stimulus on the memory-saccade. In general, the memory-saccade was strongly weighted toward the visual cue direction, yet the electrical stimulus introduced a consistent bias away from the receptive/movement field of the stimulation site. The effects of sub-threshold stimulation were consistent with a combination of vector subtraction and averaging, but not with vector summation. Vector subtraction may play a role in spatial updating of movement plans for memory-guided saccades when eye position changes during the memory period.

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1. Introduction

Many prefrontal cortical neurons, including those in the frontal eye field (FEF), are activated during tasks that require a maintained representation of a spatial location in working memory (Baddeley, 1986; Barborica & Ferrera, 2003; Funahashi, Bruce, & Goldman-Rakic, 1989; Fuster & Alexander, 1971; Fuster, Bauer, & Jervey, 1982; Goldman-Rakic, 1995a, 1995b, 1996; Kubota & Niki, 1971; Miller & Cohen, 2001; Miller & Asaad,

2002; Robins, 1996; Tomita, Ohbayashi, Nakahara, Hasegawa, & Miyashita, 1999). Several groups have found that neurons throughout dorsolateral prefrontal cortex have sustained firing during the delay interval of a memory-guided saccade task (MGS) and this activity is selective for the remembered location of the target (Constantinidis, Franowitz, & Goldman-Rakic, 2001; Funahashi et al., 1989; Funahashi, Bruce, & Goldman-Rakic, 1991; Goldman-Rakic, 1995b; Sommer & Wurtz, 2001). Spatially-selective delay activity has been regarded as a neural correlate of spatial working memory and is hypothesized to be part of a neural mechanism for the association and transformation of visual signals into voluntary movements (Courtney, Ungerleider, Kell, & Haxby, 1997; Funahashi et al., 1989; Miller, Erickson, & Desimone, 1996; Sweeney et al., 1996; Wallis &

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Miller, 2003). Similar delay activity has been identified in parietal cortex (Chafee & Goldman-Rakic, 1998; Gnadt & Anderson, 1988), thalamus (Wyder, Massoglia, & Stanford, 2003) and superior colliculus (SC; Mays & Sparks, 1980) and has been interpreted in terms of motor planning or a motor error signal. To better understand how delay activity relates to movement planning, we attempted to perturb spatial memory with subthreshold electrical stimulation of the frontal eye field.

The goal of these experiments was to shed light on the computational mechanism for translating FEF delay activity into saccades. Effects of stimulation in other areas, namely MT, have been characterized as a “winner-takes-all” (WTA) competition between electrical and visual signals (Salzman & Newsome, 1994) or as a weighted vector average (Groh, Born, & Newsome, 1997; Nichols & Newsome, 2002). These outcomes may depend on specifics of the behavioral task, e.g. Salzman and Newsome (1994) found evidence of WTA when the monkey was given discrete choices, but Nichols and Newsome (2002) found evidence for weighted vector averaging when the chosen direction was allowed to vary continuously. The computation performed may also depend on the type of eye movement made. Groh et al. (1997) found that stimulation at the same site in MT could have different effects on smooth pursuit and saccades. Hence, the “read-out” mechanism revealed by microstimulation may not correspond to a fixed computation, but rather a range of possible outcomes. The results may also show a mixture of effects, such as weighted averaging or a combination of vector averaging and subtraction.

In the present experiments, we searched for sites in the anterior bank of the arcuate sulcus where saccades could be evoked with electrical stimulation (Bruce & Goldberg, 1985; Robinson & Fuchs, 1969), and where neurons with spatially tuned delay activity could be recorded (Funahashi et al., 1989). These sites were located within or nearby the physiologically-defined Frontal Eye Field (FEF; Bruce & Goldberg, 1985), which projects to SC and to oculomotor regions of the brainstem (Helmski & Segraves, 2003; Segraves & Goldberg, 1987; Segraves, 1992; Sommer & Wurtz, 1998, 2000, 2001; Stanton, Goldberg, & Bruce, 1988), and contains a map of saccade amplitude and direction (Bruce, Goldberg, Bushnell, & Stanton, 1985). A previous study of subthreshold FEF microstimulation during memory saccades (Burman & Bruce, 1997) found that stimulation during movement execution tended to delay the production of saccades directed away from the movement field of the stimulation site, but did not investigate the effects of stimulation during the memory interval.

In the present study, we found that electrical stimulation in FEF during the delay period of a memory saccade task had weak but consistent effects on the direction, amplitude and latency of voluntary saccades.

The amplitude and direction changes were consistent with a combination of visually-weighted vector averaging and vector subtraction. Vector averaging is a possible mechanism for normalizing movement amplitude in the presence of multiple targets (Lisberger & Ferrera, 1997). The vector subtraction effect suggests that subthreshold microstimulation may initiate a spatial updating of the memory-guided saccade plan (Balan & Ferrera, 2003; Duhamel, Colby, & Goldberg, 1992; Goldberg & Bruce, 1990; Quaia, Optican, & Goldberg, 1998; Salinas, 2004; Umeno & Goldberg, 1997) or its rotational equivalent (Henriques, Klier, Smith, Lowy, & Crawford, 1998; Smith & Crawford, 2001). We speculate that subthreshold stimulation may cause the oculomotor system to behave as if the monkey had made a small saccade in the direction of the movement field of the stimulation site just prior to the memory-saccade. A preliminary version of these results has been presented in abstract form (Opris & Barborica, 2001).

2. Methods

Experiments were performed on four subadult male rhesus monkeys (*Macaca mulatta*) weighing between 6 and 9 kg. All methods were approved by the Institutional Animal Care and Use Committee at Columbia University and the New York State Psychiatric Institute. Monkeys were prepared for experiments by surgical implantation of a post used for head restraint and a recording chamber to give access to the cortex. Eye position was recorded using a monocular scleral search coil (Judge, Richmond, & Chu, 1980). All surgical procedures were performed using aseptic technique and general (isoflurane 1–3%) anesthesia. Monkeys were trained to sit in a primate chair for the duration of the experiment with their heads restrained and perform the memory-saccade task. Correct performance of the task was reinforced by liquid reward.

2.1. Visual stimulation

Fixation targets were generated and controlled by a Cambridge Research Systems VSG2/3F video frame buffer. The output from the video board was displayed on a calibrated 27 in. color monitor (Mitsubishi) with a 60 Hz non-interlaced refresh rate. The monitor stood at a viewing distance of 30 in. so that the display area subtended roughly 40 deg horizontally by 30 deg vertically. The spatial resolution of the display was 1280 pixels by 1024 lines. Fixation targets were small (0.5 deg) white squares presented on a uniform gray/black background. The luminance of the fixation target was 65.0 cd/m², while the background was close to 0 cd/m² (below the photometer threshold). The frame buffer was programmed to send out digital pulses (frame sync)

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