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The motor burst of saccade-related neurons in the deep superior colliculus during interceptive saccades

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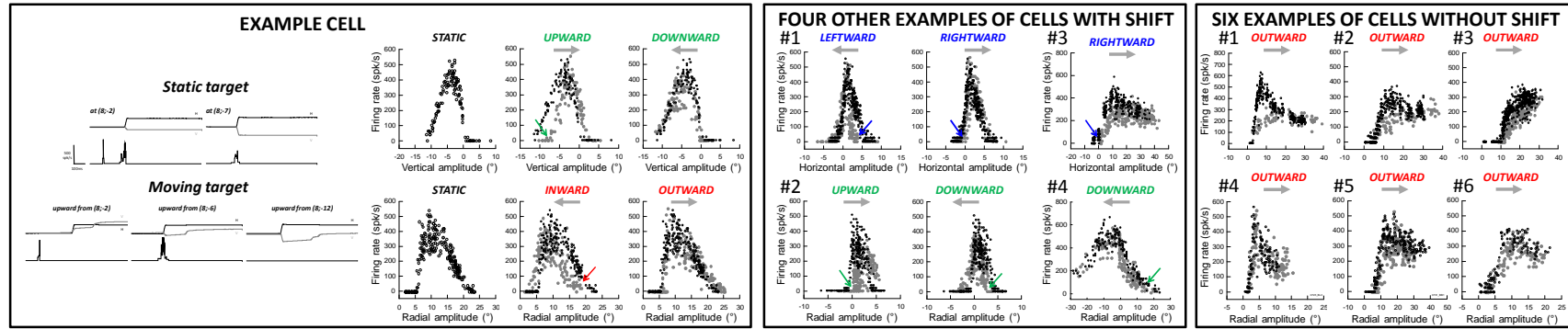
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Introduction

Given its well-established role in the orienting response and its anatomical position between cortical regions sensitive to target motions and saccade-related premotor neurons in the ponto-medullary reticular formation, the deep superior colliculus (SC) is a potential interface where commands for interceptive saccades could be issued. To date, only one study has recorded the activity of SC neurons during such saccades and found different discharge properties from those observed during saccades to stationary targets (Keller et al. 1996). Specifically, the center of the neuron's movement field (MF), i.e. the movement accompanying the most vigorous burst, shifted to larger amplitudes for saccades to targets moving away from the central visual field, in comparison to the MF center determined from saccades to stationary stimuli. This observation led to the hypothesis that during interceptive saccades, the SC motor command is supplemented by another drive downstream. However, the study did not examine the span of the neuron's MF. Changes in this property could indicate a different spatiotemporal pattern of SC activity, negating the need for an additional motor command (Fleuret et al. 2011). More recently, the suggestion was even made that a single dynamic command encoding the current and expected target location feeds the saccade oculomotor system (Fleuret and Goffart 2012). We propose that this command originates in the SC, determined by the locus of streaking activity at the time of movement execution. When the ensemble SC activity is unable to "keep up" with the moving stimulus, the motor command would be related to a target position occupied in the past.



Methods

Three rhesus monkeys generated saccades to stationary and moving targets on randomly interleaved trials. The offset of the fixation point was simultaneous with the presentation of the target in the visual periphery. The target either remained stationary (STATIC trials) or moved along the preferred axis (RADIAL trials) away from (OUTWARD) or toward the fixation point (INWARD). Vertical and horizontal target motion were also tested. The animals had to make a saccade to the target and continue to track it for few hundred msec to obtain reward. The target speed was generally 20°/sec, although other speeds (15-30-45°/s) were tested occasionally.

Eye movements were recorded with the scleral coil in magnetic field technique. Extracellular activity of 57 saccade-related SC neurons was recorded during these movements. The movement field parameters (boundaries, preferred amplitude and maximum firing rate) were estimated after spline fitting the relation between the saccade amplitude and the average firing rate during the saccade-related burst (measured from 20 ms before saccade onset to 10 ms before saccade end).

Results

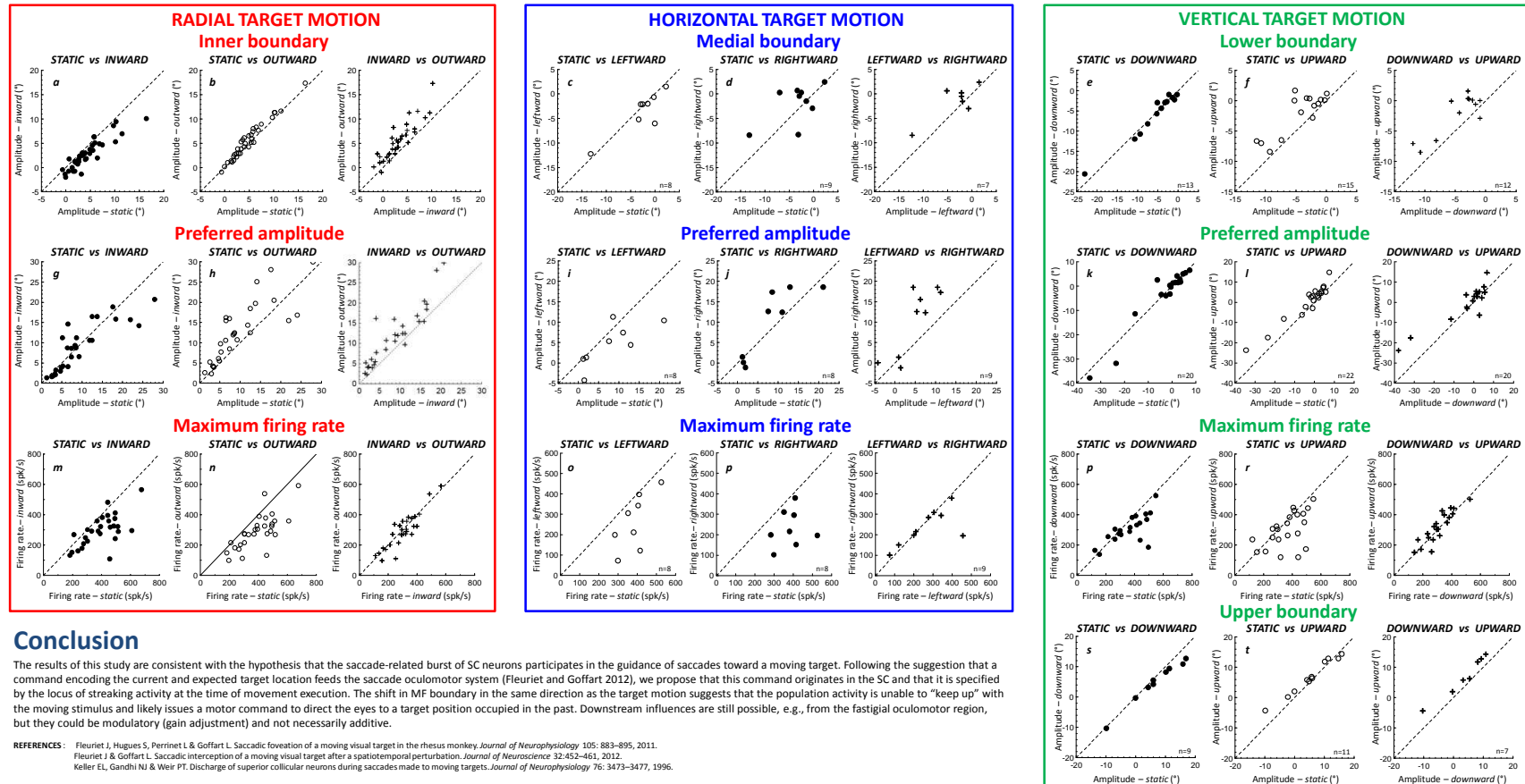
During radial target motion, the inner boundary of the MF shifted for interceptive saccades relative to saccades to a stationary stimulus. The shift was in the same direction as the target motion: toward larger saccade amplitudes for outward radial motion (mean±sd=0.7±0.8°, plot **b**) and toward smaller amplitudes for inward radial motion (-1.6±1.6°, **a**).

During vertical target motion, both lower and upper boundaries were shifted upward during upward motion of the target (2.3±2.0° and 1.1±2.0° respectively, plots **f** and **g**) whereas the upper boundary was shifted (downward) only during downward motions (-1.9±1.7°, **e**). The lower boundary was not changed (0.0±1.2°, **e**).

During horizontal target motions, the medial boundaries were not significantly changed (**c** and **d**). A shift in the preferred amplitude was significant only for outward radial motion (3.0±4.2°, **h**).

Regardless of the motion direction, the average firing rate was consistently reduced for interceptive saccades. This effect could result from the transient visual stimulation of the cells and could account for the reduction in peak velocity of interceptive saccades (not shown).

The comparison of MF features for interceptive saccades to targets moving in opposite directions (e.g., inward vs. outward) reveals that the target motion direction influences the spatiotemporal pattern of activation in the population of active neurons in the SC.



Conclusion

The results of this study are consistent with the hypothesis that the saccade-related burst of SC neurons participates in the guidance of saccades toward a moving target. Following the suggestion that a command encoding the current and expected target location feeds the saccade oculomotor system (Fleuret and Goffart 2012), we propose that this command originates in the SC and that it is specified by the locus of streaking activity at the time of movement execution. The shift in MF boundary in the same direction as the target motion suggests that the population activity is unable to "keep up" with the moving stimulus and likely issues a motor command to direct the eyes to a target position occupied in the past. Downstream influences are still possible, e.g., from the fastigial oculomotor region, but they could be modulatory (gain adjustment) and not necessarily additive.

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