



# Microsaccade production during saccade cancellation in a stop-signal task



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## ARTICLE INFO

### Article history:

Received 10 July 2014

Received in revised form 13 October 2014

Available online 6 November 2014

### Keywords:

Rostral superior colliculus

Frontal eye field

Fixation neurons

Premotor theory of attention

Response inhibition

## ABSTRACT

We obtained behavioral data to evaluate two alternative hypotheses about the neural mechanisms of gaze control. The “fixation” hypothesis states that neurons in rostral superior colliculus (SC) enforce fixation of gaze. The “microsaccade” hypothesis states that neurons in rostral SC encode microsaccades rather than fixation *per se*. Previously reported neuronal activity in monkey SC during the saccade stop-signal task leads to specific, dissociable behavioral predictions of these two hypotheses. When subjects are required to cancel partially-prepared saccades, imbalanced activity spreads across rostral and caudal SC with a reliable temporal profile. The microsaccade hypothesis predicts that this imbalance will lead to elevated microsaccade production biased toward the target location, while the fixation hypothesis predicts reduced microsaccade production. We tested these predictions by analyzing the microsaccades produced by 4 monkeys while they voluntarily canceled partially prepared eye movements in response to explicit stop signals. Consistent with the fixation hypothesis and contradicting the microsaccade hypothesis, we found that each subject produced significantly fewer microsaccades when normal saccades were successfully canceled. The few microsaccades escaping this inhibition tended to be directed toward the target location. We additionally investigated interactions between initiating microsaccades and inhibiting normal saccades. Reaction times were longer when microsaccades immediately preceded target presentation. However, pre-target microsaccade production did not affect stop-signal reaction time or alter the probability of canceling saccades following stop signals. These findings demonstrate that imbalanced activity within SC does not necessarily produce microsaccades and add to evidence that saccade preparation and cancellation are separate processes.

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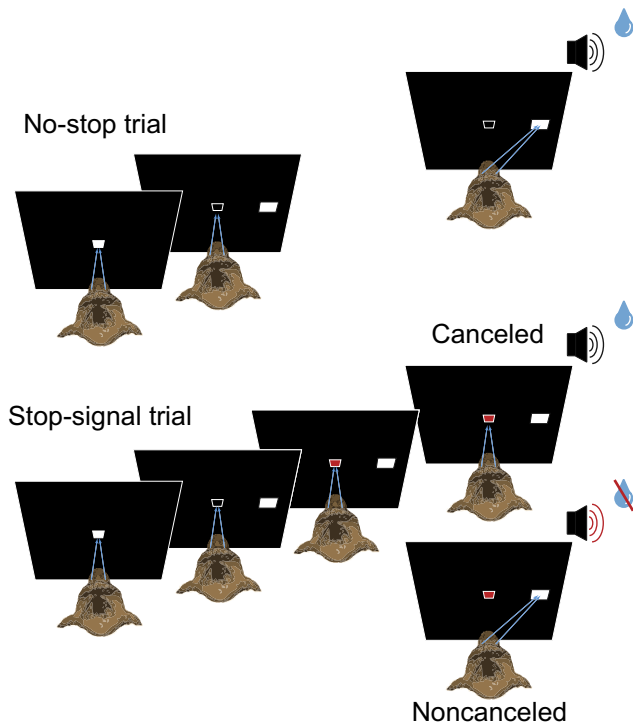
## 1. Introduction

The saccade stop-signal task has provided tremendous insight into the neurophysiological basis of eye movements (Asrress & Carpenter, 2001; Atsma et al., 2014; Bissett & Logan, 2013; Born, Mottet, & Kerzel, 2014; Boucher et al., 2007; Brown et al., 2008; Cabel et al., 2000; Camalier et al., 2007; Corneil & Elsley, 2005; Emeric et al., 2007; Goonetilleke, Wong, & Corneil, 2012; Gulberti, Arndt, & Colonius, 2014; Hanes & Carpenter, 1999; Hanes & Schall, 1995, 1996; Joiner, Lee, & Shelhamer, 2007; Kornyllo et al., 2003; Lo et al., 2009; Logan & Irwin, 2000; Morein-Zamir & Kingstone, 2006; Pouget et al., 2011; Ray, Pouget, & Schall, 2009; Scangos & Stuphorn, 2010; Stevenson, Elsley, & Corneil, 2009; Stuphorn, Brown, & Schall, 2010; Walton

& Gandhi, 2006; Wessel, Reynoso, & Aron, 2013; Wong-Lin et al., 2010). Participants are occasionally instructed to cancel saccades shortly after a cue to respond (Fig. 1). By analyzing subjects' accuracy and reaction times as the outcome of a race between go and stop processes, investigators can estimate the time required for subjects to inhibit actions (Logan, 1994; Logan & Cowan, 1984). This metric, referred to as stop-signal reaction time (SSRT), specifies the duration in which neurons participate in initiating or withholding motor responses. Investigators have reported detailed profiles of neural activity recorded from many ocular motor structures during the saccade stop-signal task (Hanes, Patterson, & Schall, 1998; Stuphorn, Brown, & Schall, 2010; see also Brunamonti, Thomas, & Paré, 2008; Mirabella, Pani, & Ferraina, 2011; Murthy, Ray, Shorter, Schall, & Thompson, 2009; reviewed by Schall & Godlove, 2012a), and these data can be used to generate novel predictions about oculomotor behavior. For instance, when monkeys inhibit eye movements during the stop-signal task, pools of neurons in caudal and rostral superior colliculus (SC) are

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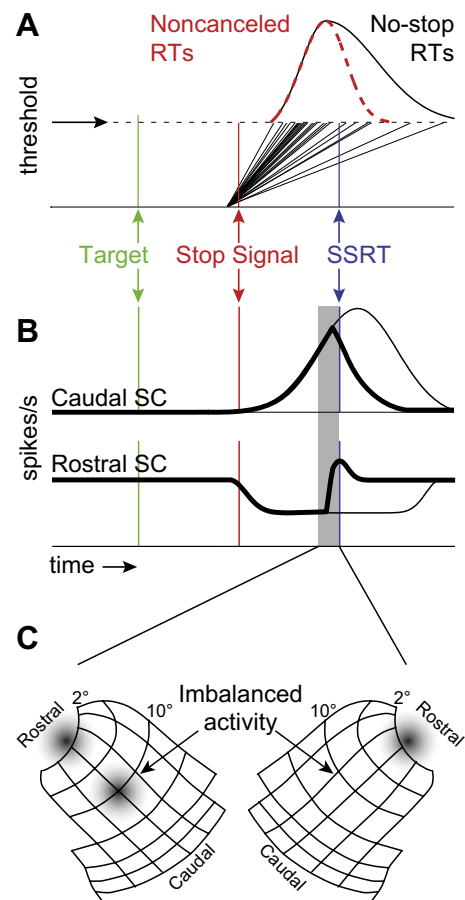


**Fig. 1.** The saccadic stop-signal (countermanding) task. Top: No-stop trials were initiated when monkeys fixated a central point. After a variable time, the center of the fixation point was extinguished leaving an outline. A peripheral target was presented simultaneously at one of two possible locations. Monkeys were required to fixate targets with quick saccades. On correct trials, a speaker sounded a tone indicating success and a juice reward was delivered. Bottom: Stop-signal trials were initiated in the same way. After a variable time (SSD), the center of the fixation point was reilluminated in a different color, instructing the monkeys to withhold movement. Successful inhibition of saccades resulted in rewarded Canceled trials, but errant saccades resulted in unrewarded Noncanceled trials accompanied by a different speaker tone.

simultaneously active before and during SSRT producing an imbalance across the saccade trajectory map in this area (Paré & Hanes, 2003; Fig. 2). As detailed below, these data lead to predictions about the patterns of microsaccades that should be elicited when monkeys cancel saccades during the stop-signal task.

It is well-accepted that neurons in the intermediate layers of SC encode target positions and are arranged in an orderly saccade polar coordinate map (Gandhi & Katnani, 2011; Krauzlis, 2008; Lee, Rohrer, & Sparks, 1988; Munoz & Schall, 2004; Munoz et al., 2000; Robinson, 1972). But disagreement persists about the function of neurons in rostral SC at the origin of this coordinate system. An early line of work indicated that neurons in rostral SC enforce fixation (Büttner-Ennever et al., 1999; Gandhi & Keller, 1997; Munoz, Waizman, & Wurtz, 1996; Munoz & Wurtz, 1993a, 1993b; Paré & Guitton, 1994). According to this view, neurons in the rostral pole of SC inhibit saccades regardless of the activity level of neurons in caudal SC. This view assumes the existence of two different neuron types in SC, one responsible for gaze-shifting and another responsible for gaze-holding. To describe the function of the rostral SC, we will refer to this as the *fixation hypothesis*.

More recent work emphasizes the contribution of all neurons in the intermediate layers of SC to gaze-shifting (Goffart, Hafed, & Krauzlis, 2012; Hafed, Goffart, & Krauzlis, 2008; Hafed & Krauzlis, 2012; Krauzlis, Basso, & Wurtz, 1997). According to this view, neurons in rostral SC simply contribute to saccades near the point of fixation, and gaze-holding is accomplished by maintaining equilibrium across the saccade map. When the equilibrium of SC activity becomes imbalanced toward a target location (as illustrated in



**Fig. 2.** Timing and spatial distribution of imbalanced activity in superior colliculus (SC) during the stop-signal task. (A) Application of Logan's race model to reaction time and accuracy data yields estimates of stop-signal reaction time (SSRT blue). This is the median time necessary for movements to be canceled. Given the presentation of a stop-signal on a particular trial, motor processes on trajectory to reach threshold after SSRT will not result in movement, effectively truncating the reaction time distribution. (B) Imbalanced activity in SC shows a predictable spatial and temporal evolution during the saccade stop-signal task. Thick traces represent activity on canceled trials. Thin traces depict activity on latency matched no-stop trials. Diagram is adapted from data presented by Paré and Hanes (see their Figs. 3 and 7). (C) Spatial activity in SC is stereotyped around SSRT. Putative neural activity is taken from gray window in (B). Rostral and caudal SC show coactivation just before and concomitant with SSRT on canceled trials.

Fig. 2C) microsaccades or larger gaze shifts are initiated. To describe the function of the rostral SC, we will refer to this as the *microsaccade hypothesis*.

Given the pattern of activity that was previously reported in SC when monkeys canceled eye movements during the stop-signal task (Paré & Hanes, 2003; see also Hanes, Patterson, & Schall, 1998), the microsaccade hypothesis and fixation hypothesis make different predictions about the pattern of microsaccades that should be observed before and during SSRT. The microsaccade hypothesis predicts that imbalanced activity in SC during the interval that normal saccades are inhibited (i.e. SSRT) will lead to increased microsaccade production with most directed toward the target. The fixation hypothesis predicts that elevated activity of gaze-holding neurons in rostral SC will lead to decreased microsaccade production.

To test predictions of the microsaccade and fixation hypotheses explicitly, we used high-resolution eye tracking and analysis techniques to record micro- and normal saccades from four monkeys trained to perform the saccade stop-signal task. The use of monkeys instead of humans provides several advantages. They were highly trained and would readily complete thousands of trials

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