

# Activity in the Primate Rostral Superior Colliculus during the “Gap Effect” for Pursuit and Saccades

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**KEYWORDS:** superior colliculus; pursuit; saccade; gap effect; latency

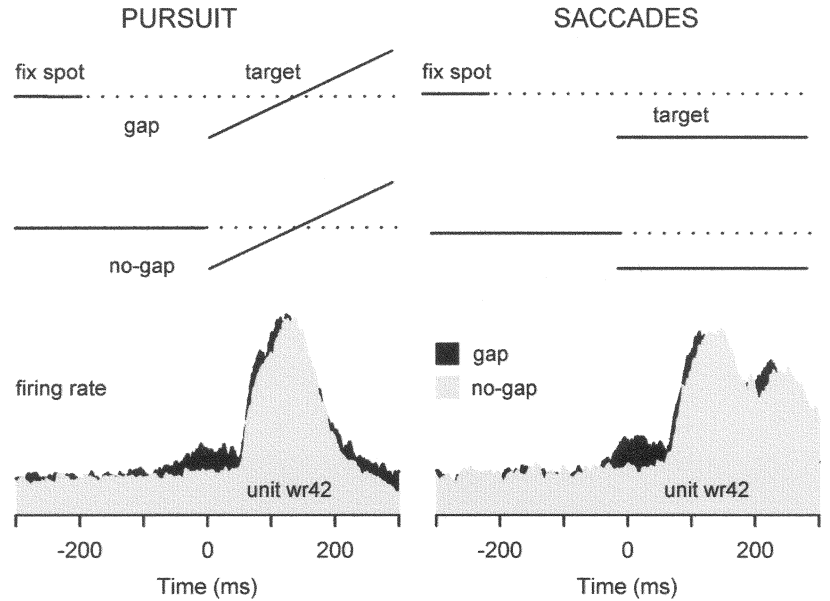
The latencies of both pursuit and saccadic eye movements are reduced when a fixated visual target is extinguished several hundred milliseconds before a new target appears.<sup>1–6</sup> One possible neural substrate for this “gap effect” is the rostral superior colliculus (SC), which has recently been shown to participate in pursuit eye movements, in addition to its established role in the control of saccades. The discharge rate of buildup neurons in the rostral SC (rSC) is related to the retinal position of targets during pursuit, as well as during the preparation and execution of saccades.<sup>7,8</sup> In addition, microstimulation of the rSC disrupts the initiation of both types of eye movements.<sup>9</sup> To test whether these rostral buildup neurons could underlie the “gap effect,” we have now studied their activity with this paradigm during both pursuit and saccades.

Monkeys tracked a target stimulus that appeared either immediately after the offset of the fixation spot (no-gap trials) or 200 msec after the offset of the fixation spot (gap trials). On saccade trials, the target stimulus was stationary and was presented at an eccentricity of  $\sim 3.5^\circ$  along the horizontal meridian. On pursuit trials, the target stimulus appeared at an eccentricity of  $\sim 2^\circ$  and moved toward the center of the display at  $15^\circ/\text{sec}$ . We adjusted the starting position of the stimulus to produce saccade-free pursuit and chose neurons with appropriate response fields. We identified the neurons in our sample ( $n = 72$ ) as rostral buildup neurons on the basis of criteria described previously.<sup>7</sup>

The activity of most rostral buildup neurons showed a “gap effect” for both pursuit and saccades. For example, on no-gap trials, the firing rate of the neuron illustrated in FIGURE 1 remained nearly constant at 25 spikes/sec until 50–100 msec after target onset, at which point the firing rate increased to more than 100 spikes/sec. However, on gap trials, the firing rate of this neuron increased after the offset of the fixation spot, reaching a firing rate of 40–50 spikes/sec. These changes in activity

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*Ann. N.Y. Acad. Sci.* 956: 409–413 (2002). © 2002 New York Academy of Sciences.

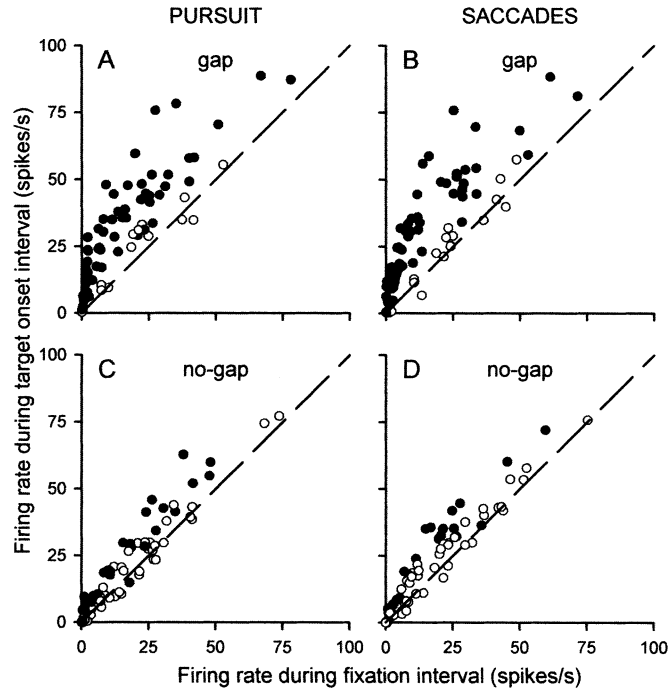


**FIGURE 1.** Activity of a sample rostral SC buildup neuron during pursuit and saccade trials. At top, traces indicate the timing of fixation spot offset and target onset. *Solid lines* indicate positions of visible stimuli; *dotted lines* indicate positions of stimuli no longer visible. At bottom, average firing rates from gap (*black*) and no-gap (*gray*) trials are shown superimposed. These represent the average activity from 40 gap and 64 non-gap trials during pursuit, and 35 gap and 34 non-gap trials during saccades. The *vertical scale bar* indicates 150 spikes/s.

were most notable around the time of target onset (defined as 0 msec), well before the onset of either pursuit or saccades. To quantify these changes in activity, we measured the activity in two epochs: (1) a “target onset” interval defined as 50 msec before target appearance to 50 msec after target appearance, and (2) a “fixation” interval defined as either the final 100 msec before the fixation spot was extinguished (gap trials) or a matching 100-msec interval starting 300 msec before the fixation spot was extinguished (no-gap trials).

As shown by the scatter plots in FIGURE 2, on gap trials most neurons in our sample had higher activity at target onset than during fixation. We found a significant difference in activity for 57 of 72 neurons prior to the onset of pursuit (solid symbols in FIG. 2A) and 53 of 72 neurons prior to the onset of saccades (FIG. 2B). In contrast, on no-gap trials, we found a significant difference for only 29 of 72 neurons for pursuit (FIG. 2C) and 23 of 72 neurons for saccades (FIG. 2D). This difference in the activity shows that rostral buildup neurons could represent the neural correlate of the behavioral “gap effect” observed previously for both pursuit and saccades.

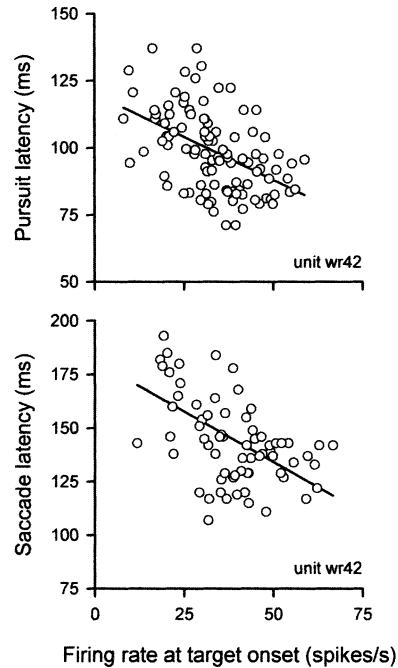
To test whether these gap-related changes in activity were related to latency, we performed a linear regression analysis between the latency and firing rate measurements pooled across gap and no-gap trials. The results of this analysis for one sam-



**FIGURE 2.** Summary of rostral buildup neuron activity during gap and non-gap trials. Average firing rate at target onset interval is plotted as a function of the average firing rate during fixation for gap (**A**) and no-gap (**C**) pursuit trials, and for gap (**B**) and no-gap (**D**) saccade trials. *Solid symbols* indicate significant differences between the two intervals (Wilcoxon rank sum test,  $p < 0.05$ ). Data from a total of 72 neurons are shown in each plot.

ple neuron (the same as in FIGURE 1) are shown in FIGURE 3. Pursuit and saccade latencies both exhibited significant negative correlations with firing rate ( $r = -0.49$  and  $-0.53$  for pursuit and saccades, respectively). Thus, increases in the activity of this rostral buildup neuron were correlated with the decreases in the latency of pursuit and saccades associated with the “gap effect.” Across our sample of neurons, significant negative correlations were found for 25 of 72 neurons for pursuit and 44 of 72 neurons for saccades. Notably, 80% of the neurons that exhibited a significant negative correlation for pursuit also showed a significant negative correlation for saccades (20 of 25).

Our results show that most buildup neurons in the rostral SC increase their activity in the presence of a “gap” prior to either pursuit or saccades. These results indicate that a common process of motor preparation or release of fixation involving the rostral SC could be responsible for the previous findings of a behavioral “gap effect” for both pursuit and saccades.<sup>1–6</sup> The presence of such shared neural processing confirms the suggestion, based on behavioral evidence, that the two types of eye movements have shared inputs.<sup>5</sup> Although the function of these rostral buildup neurons remains unsettled, the increased activity we observed in the presence of a “gap”



**FIGURE 3.** Correlation between latency and firing rate at target onset for pursuit (*top*,  $n=104$ ) and saccades (*bottom*,  $n=69$ ) for the same neuron shown in FIGURE 1. Each symbol indicates a pair of measurements from one trial. The correlations for this neuron from pursuit ( $-0.49$ ) and saccade ( $-0.53$ ) trials were both significant ( $p < 0.05$ , ANOVA).

could act to speed the initiation of both types of eye movements toward a common visual target.

#### ACKNOWLEDGMENTS

This work was supported by NIH Grant EY12212 and by the McKnight Foundation.

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