

Comment on “Tracking an Invisible Target Reveals Spatial Tuning of Neurons in the Rostral Superior Colliculus Is Not Dependent on Visual Stimuli”

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We thank Van Horn for her interesting review of our results. She has nicely described key aspects of our data and identified important questions prevailing in the field. In this comment, we would like to clarify two important points.

Are the neurons reported in Hafed & Krauzlis (2008) the same rostral SC neurons as those studied by others? It is always a concern that different studies might sample different sets of neurons but give them the same name. We think that this is unlikely in our case, because we characterized the activity of neurons using behavioral tasks and firing rate measurements based on those proposed by the original description of “fixation neurons” (Munoz & Wurtz, 1993). Also, the differences between microstimulation results referred to by Van Horn have fairly straightforward explanations and should not be taken as evidence that we studied different classes of neurons. We applied stimulation unilaterally while the monkeys were instructed to fixate, whereas the other cited experiments often involved bilateral stimulation while the monkeys generated saccades. Together, these results indicate that stimulation of the rostral SC, like other locations in the SC, can evoke eye movements when done in isolation but cause “averaging” saccades when done in combination with visually guided eye movements (as also shown in Gandhi & Keller, 1999; Basso *et al.*, 2000). It is also true that our neurons were tuned for small eccentricities during saccades and smooth pursuit, whereas Munoz & Wurtz (1993) reported that some of the “fixation” neurons paused for saccades in all directions. This difference is likely due to the saccade amplitudes that were tested, rather than differences in neurons. Munoz and Wurtz (and others) were mostly concerned with larger saccades and did not study movements smaller than $\sim 1^\circ$. More recently, we investigated rostral SC activity during microsaccades and found evidence of spatial tuning for extremely small retinal eccentricities (often less than 12-15 min arc) even for neurons that appeared to pause for voluntary saccades of all (tested) directions and amplitudes (Hafed *et al.*, in press).

Does the SC encode “foveal goal location” (or “zero error”)? Yes – our results indicate that this corresponds to the case when activity across the left and right rostral SC is balanced (Hafed *et al.*, 2008), i.e. when a target is foveated. Also, as shown in Krauzlis *et al.* (1997), even though the peaks of the tuning curves for neurons in the rostral SC predominantly cover foveal/parafoveal locations on the contralateral side, the peaks for some neurons cross the midline to participate in the encoding of targets located in the ipsilateral side as well. Thus, not only does the SC map on each side include “zero”, it also extends to foveal locations in the opposite hemifield (also see Hafed *et al.*, in press). This indicates that the distributed population coding scheme that exists in the SC (Lee *et al.*, 1988) also extends into the rostral region, allowing the population of neurons to represent “zero error” (also see Figs. 9, 11 of Hafed & Krauzlis, 2008). We prefer using the term “goal location” as opposed to “motor” or “position error” because it has been shown that SC activity is involved in target selection (McPeck & Keller, 2004; Carello & Krauzlis, 2004), not just in the execution of saccades. Indeed, in the case of smooth pursuit, SC microstimulation biases selection in favor of the moving target that starts at the matching retinotopic location encoded by the stimulated neurons, even though the subsequent movement is in the direction opposite to that predicted by the “position error” interpretation (Carello & Krauzlis, 2004).

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