Reassessing the location of motor activity in the Superior Colliculus map during adaptation.

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Introduction

The deeper layers of the Superior Colliculus (SC) are an important part of the system involved in producing and controlling saccades, the rapid conjugate eye movements that redirects the line of sight to align the fovea on the target of interest. In the presence of a visual stimulus, motor-related activity in the SC results in saccade. The locus of this activity in the SC determines the direction and amplitude of the movement (fig.1).

If the conditions in which the movements are produced change or are manipulated, the accuracy of the movements can be affected. Over time, the movements are altered to reduce the residual visual error. The contribution of the SC to these adaptations remains unclear. Repeated visual error at the end of the movements could lead to a change in the locus of activity within the SC. This would result in a new motor output determined by the new active population (fig. 2). A recent study supporting this hypothesis reports that the activity of some neurons in SC changed during saccade adaptation, suggesting that theses changes might by mediated through the SC (Takeichi et al., 2007).

Alternatively, the locus of activity in the SC could remain unchanged, specifying a movement related to the target displacement (fig. 3), as reported by a previous study suggesting that the movements are altered without changing the motor command (Frens and van Opstal, 1997).

Location of the active population in the SC determines the amplitude of the eye movement.

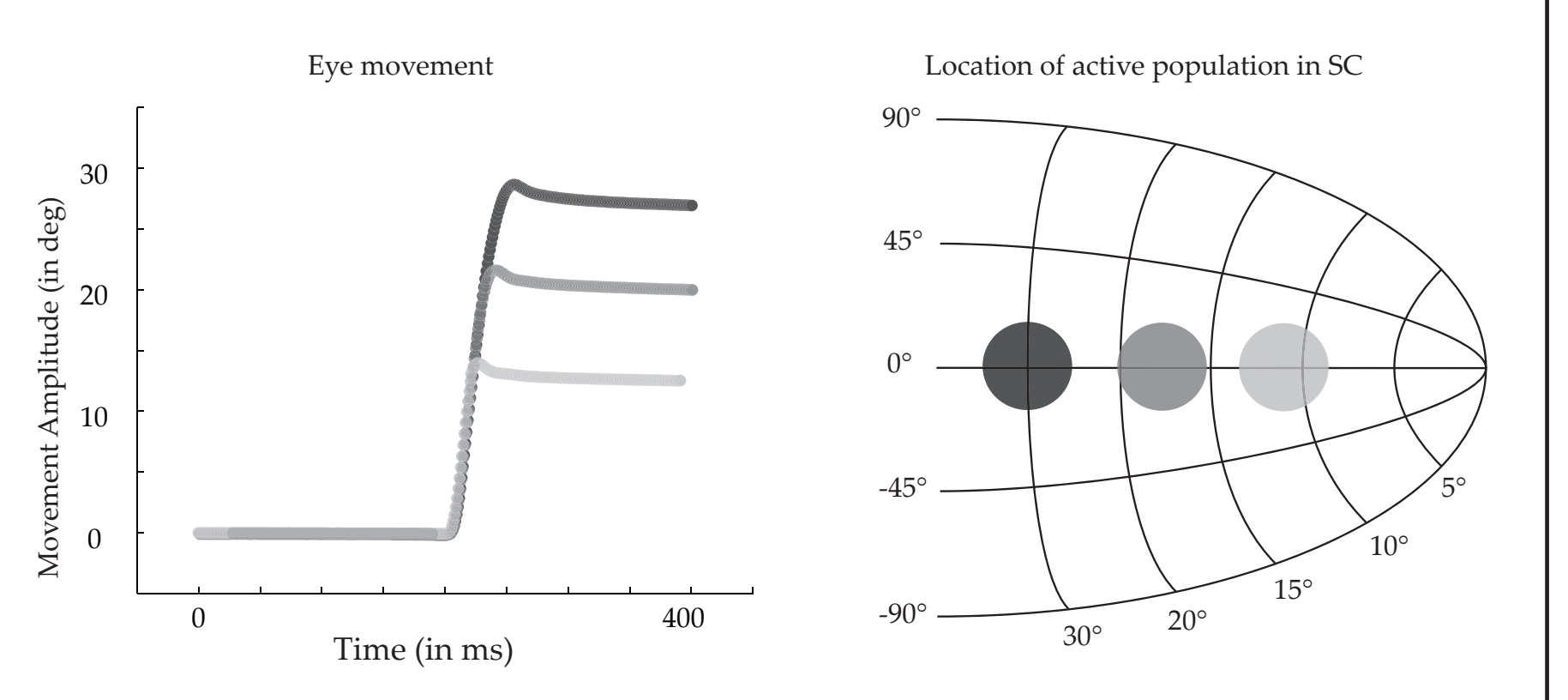

Figure 1 Example of eye movements of 3 different amplitudes (left panel) and schematics of the corresponding locus of activation in the deep layers of the SC (right panel).

Hypothesis 1
Change in the locus of activity in the SC is specifying the direction and amplitude of the observed movement

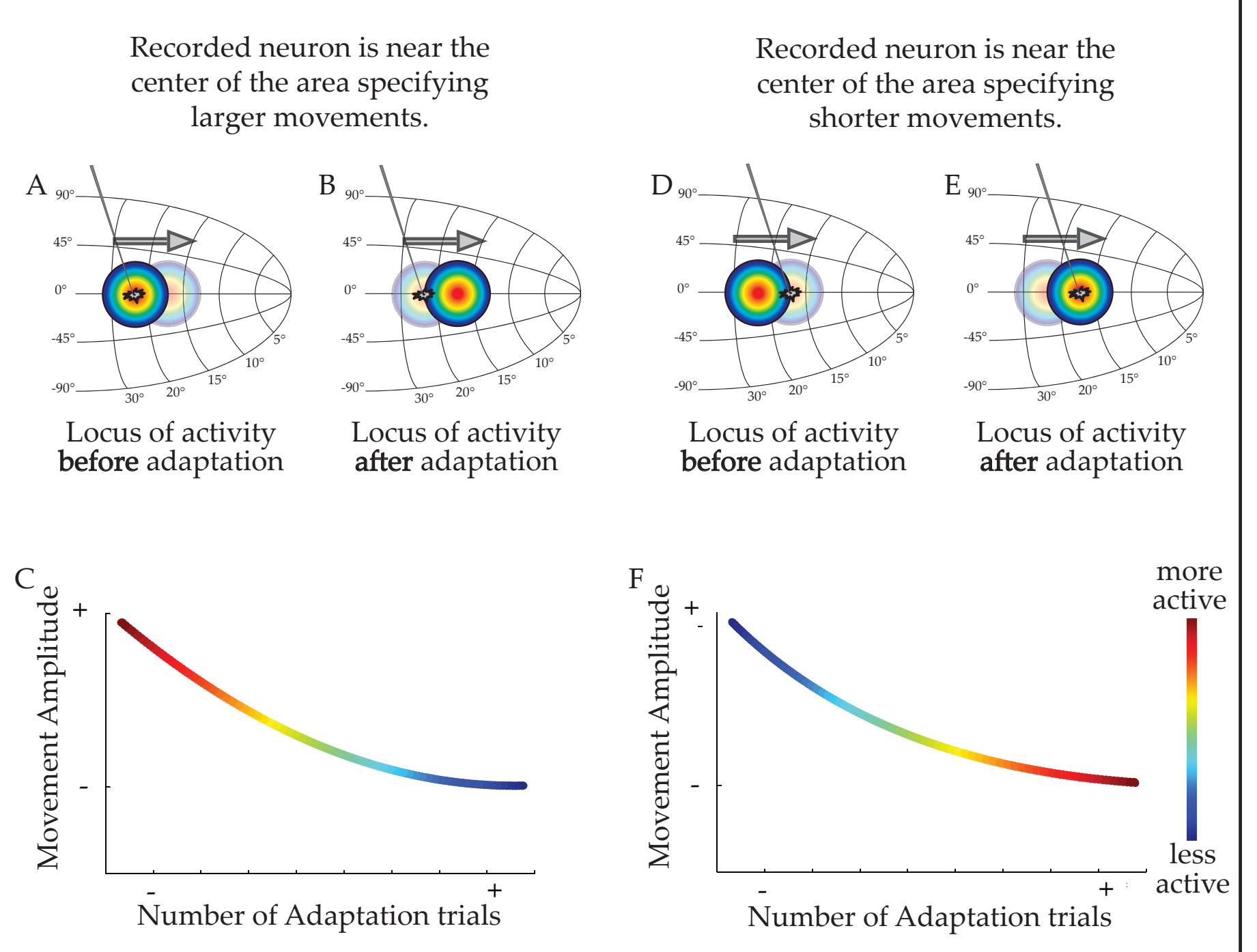

Figure 2 Representation of the activity in the SC neurons during adaptation if the SC is involved in the adaptation mechanisms.
On the left, the recorded neuron is located near the center of the area responsible for movements of the amplitude of the initial movement, thus producing a vigorous burst of activity (A). When a visual error is introduced experimentally, the movement has to be altered. The locus of activity within SC gradually moves to a more rostral location, specifying shorter movements (B). The recorded neuron contributes only marginally to this new active population. Panel C illustrates what should be observed during adaptation if the SC is involved. As the number of movements increases, the amplitude decreases and the neuron becomes less active.
On the right, the recorded SC neuron is located in an area responsible for movements of smaller amplitude than the initial movement and is contributing weakly to that population (D). Once again, the locus of activity within SC gradually moves rostrally to produce shorter movements (E). However, in this situation, the neuron is near the center of the new active population and contributes greatly to it. As panel F indicates, in this case, the neuron becomes more active as the adaptation progresses.

Hypothesis 2
Locus of activity in the SC remains unchanged and specifies the desired displacement based on the location of the visual target.

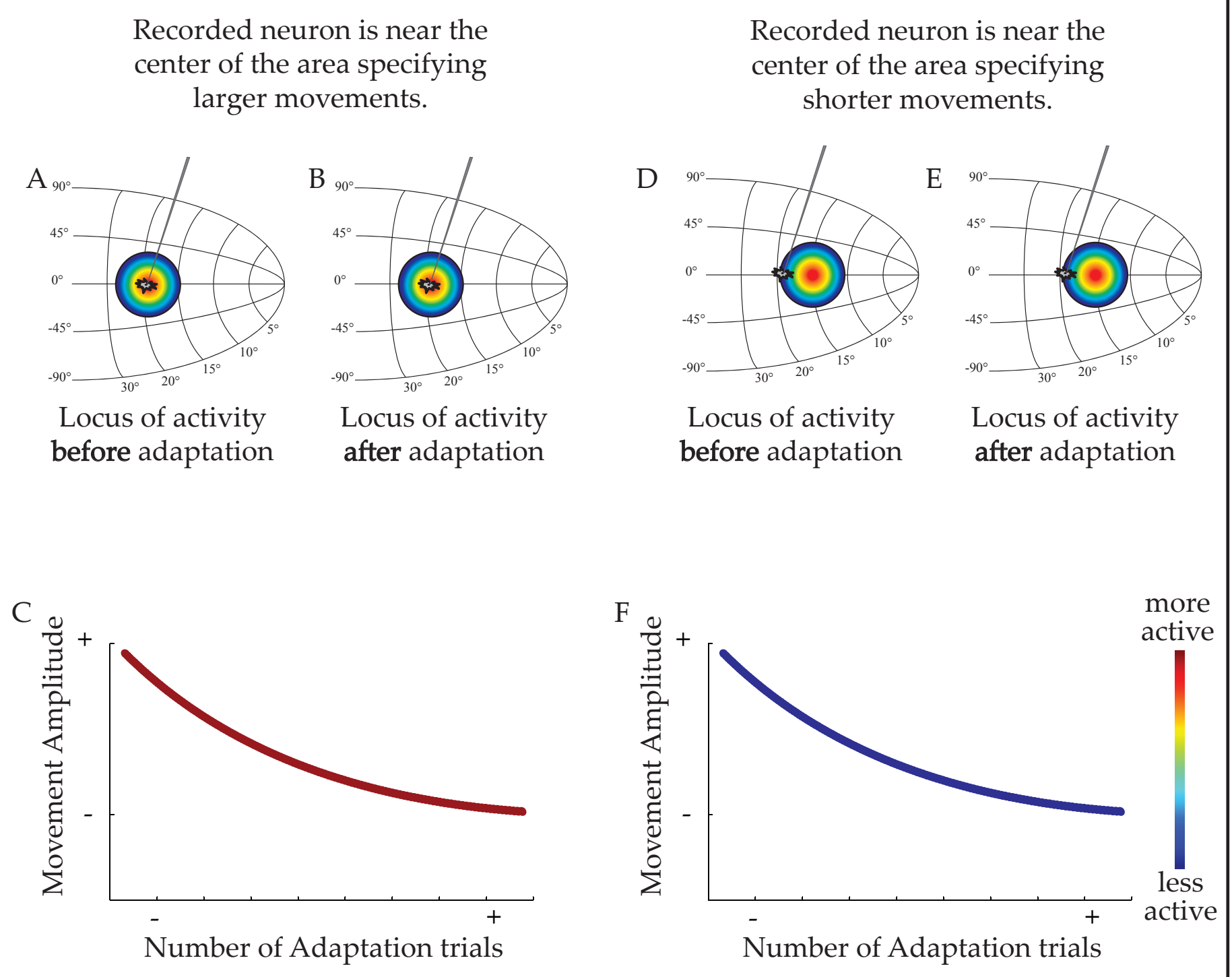

Figure 3 Representation of the activity in the SC neurons during adaptation if the SC is not involved in the adaptation mechanisms.
On the left, the recorded SC neuron is located near the center of the area responsible for movements of the amplitude of the initial movement, thus producing a vigorous burst of activity (A). When a visual error is introduced experimentally, the locus of activity within SC does not change. It still specifies a movements to the visual target (B). Panel C illustrates what activity should be observed during adaptation if the SC is not involved. As the adaptation progresses, the movements become more altered and their amplitude decreases but the recorded neuron keeps a level of activity representative of the target displacement, not the observed movement. On the right, the recorded SC neuron is located in an area responsible for movements of smaller amplitude than the initial movement and is contributing weakly to that population (D). Once again, despite the fact that the locus of activity within SC remains unchanged (E), the movements are altered and their amplitude decreases (F). The neuron's activity still represents the target displacement, not the observed movement.

Methods

20 neurons were recorded in the deeper layers of SC. Once a neuron was isolated, its movement field was assessed by presenting visual targets at various locations in contralateral visual hemifield. During that phase, the subject was trained to fixate on an illuminated LED (Fixation). During this fixation, a second LED (Target1) was illuminated. After a brief delay, the first LED was turned off providing the cue to release fixation and initiate the eye movement toward Target1. Soon after the onset of the saccade, Target1 was turned off so there was no visual feedback provided at the end of the movement (Probe Trials fig.4A).

The adaptation was induced using a variant of the McLaughlin (1967) saccade adaptation task. To avoid having mutiple motor bursts, only backward adaptation was used. The first part of the task was identical to the Probe Trials, but 20-40ms after Target1 was turned off, a second target (Target2) was illuminated. Target2 was located along the same vector as Target1 but at about half the eccentricity, causing the appearance of a visual error at the end of the initial movement and leading to a corrective movement back to Target2 (Adaptation Trials fig.4B).

Representation of the trials used

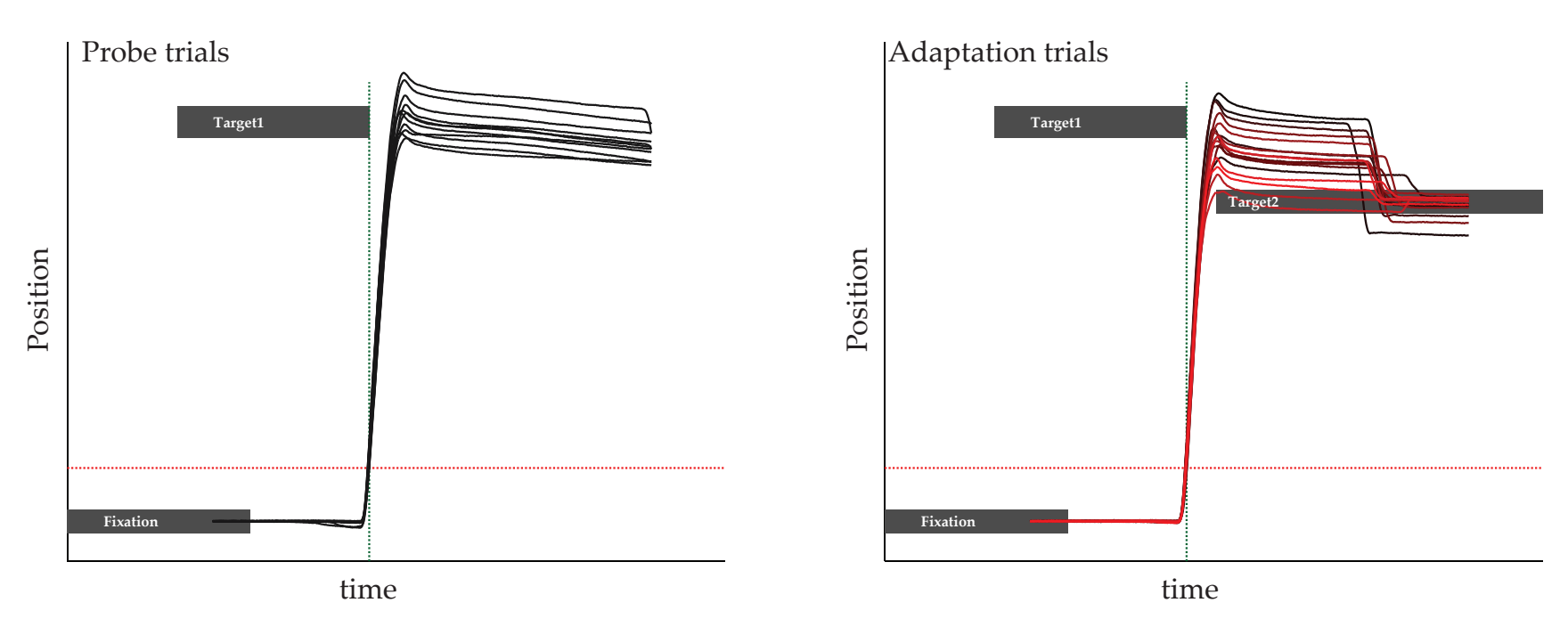

Figure 4 Probe Trials. Thick gray traces indicate the Fixation and Target1 timing and location. Thin black lines show eye postion during some Probe trials. When the movement breaks the amplitude window (red dotted line), Target1 is turned off (timing indicated by green dotted line). Adaptation Trials. Thick gray traces indicate the Fixation, Target1 and Target2 timing and location. Thin black to red lines show examples of eye movements during Adaptation trials. Amplitude window indicated by red dotted line. Time when Target1 is turned off indicated by green dotted line.

Recorded neuron is near the center of the area specifying movements Target1.

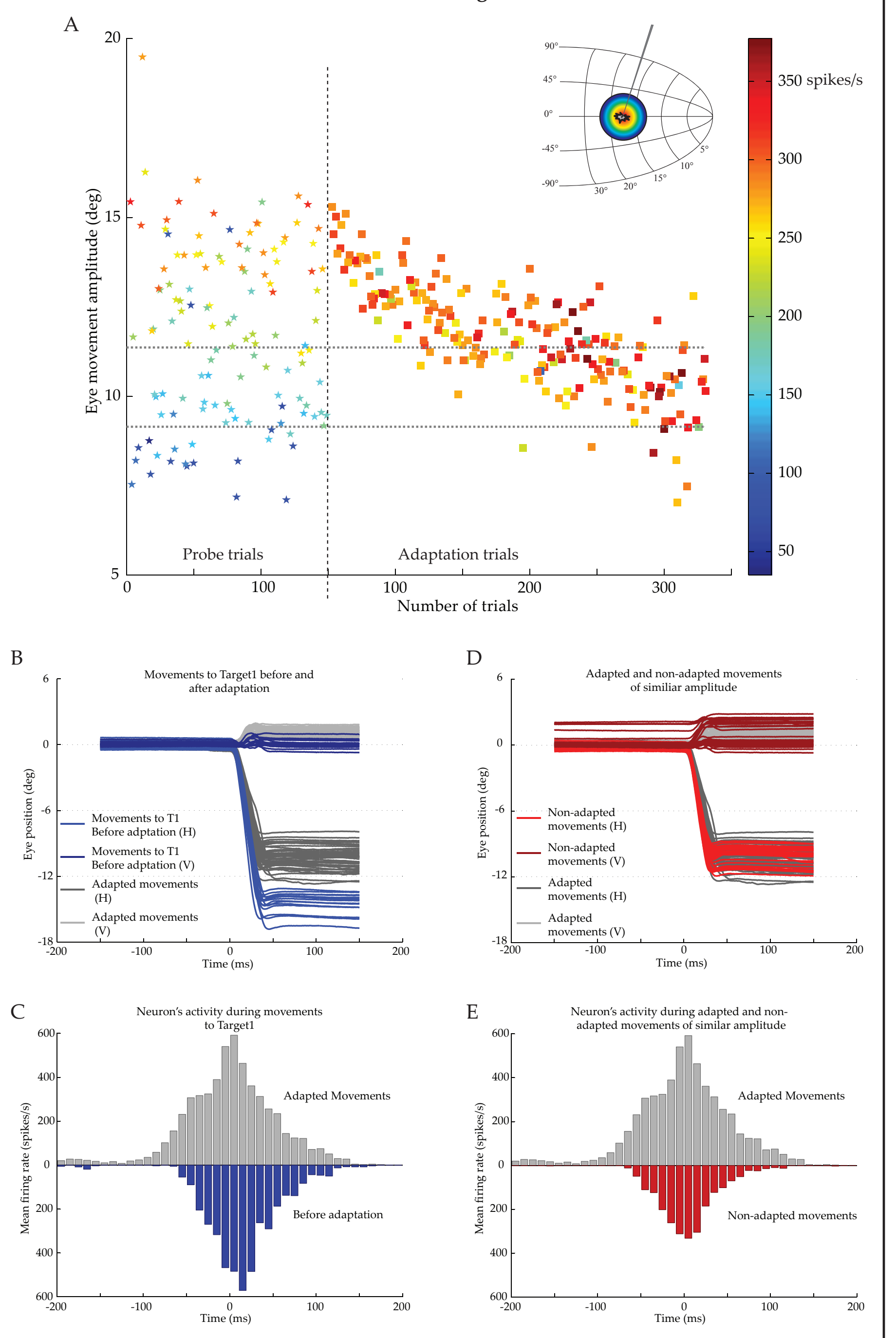

Figure 5 A- Example of a neuron that displayed vigorous bursts of activity for movements of ~15 degrees and weak bursts for shorter movements in the pre-adaptation phase (star symbols). Solid squares indicate adaptation trials. B- Eye position traces of adapted movements to Target1 (gray) and of movements to Target1 in the pre-adaptation phase (blue). C- Neuron's activity during adapted movements to Target1 (gray) and during movements to Target1 in the pre-adaptation phase (blue). D- Eye position traces of adapted movements to Target1 (gray) and of movements of similar amplitude from the pre-adaptation phase. E- Neuron's activity during adapted movements to Target1 (gray) and during movements of similar amplitude from the pre-adaptation phase.

Recorded neuron is near the edge of the area specifying movements Target1.

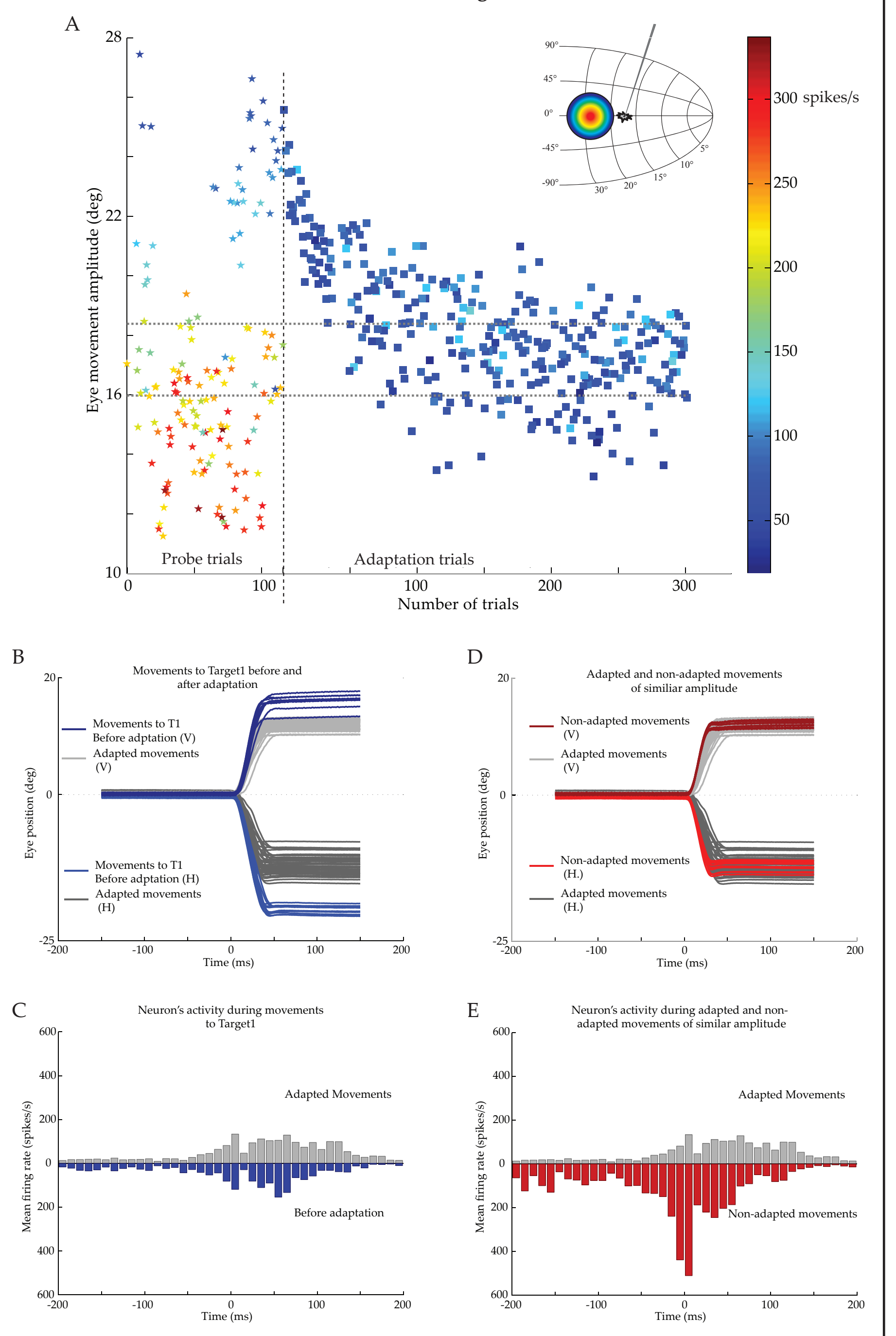

Figure 6 A- Example of a neuron that displayed vigorous bursts of activity for short movements and weak bursts for larger movements in the pre-adaptation phase (star symbols). Solid squares indicate adaptation trials. B- Eye position traces of adapted movements to Target1 (gray) and of movements to Target1 in the pre-adaptation phase (blue). C- Neuron's activity during adapted movements to Target1 (gray) and during movements to Target1 in the pre-adaptation phase (blue). D- Eye position traces of adapted movements to Target1 (gray) and of movements of similar amplitude from the pre-adaptation phase. E- Neuron's activity during adapted movements to Target1 (gray) and during movements of similar amplitude from the pre-adaptation phase.

Neurons' activity during adaptation away from the center of its movement field.

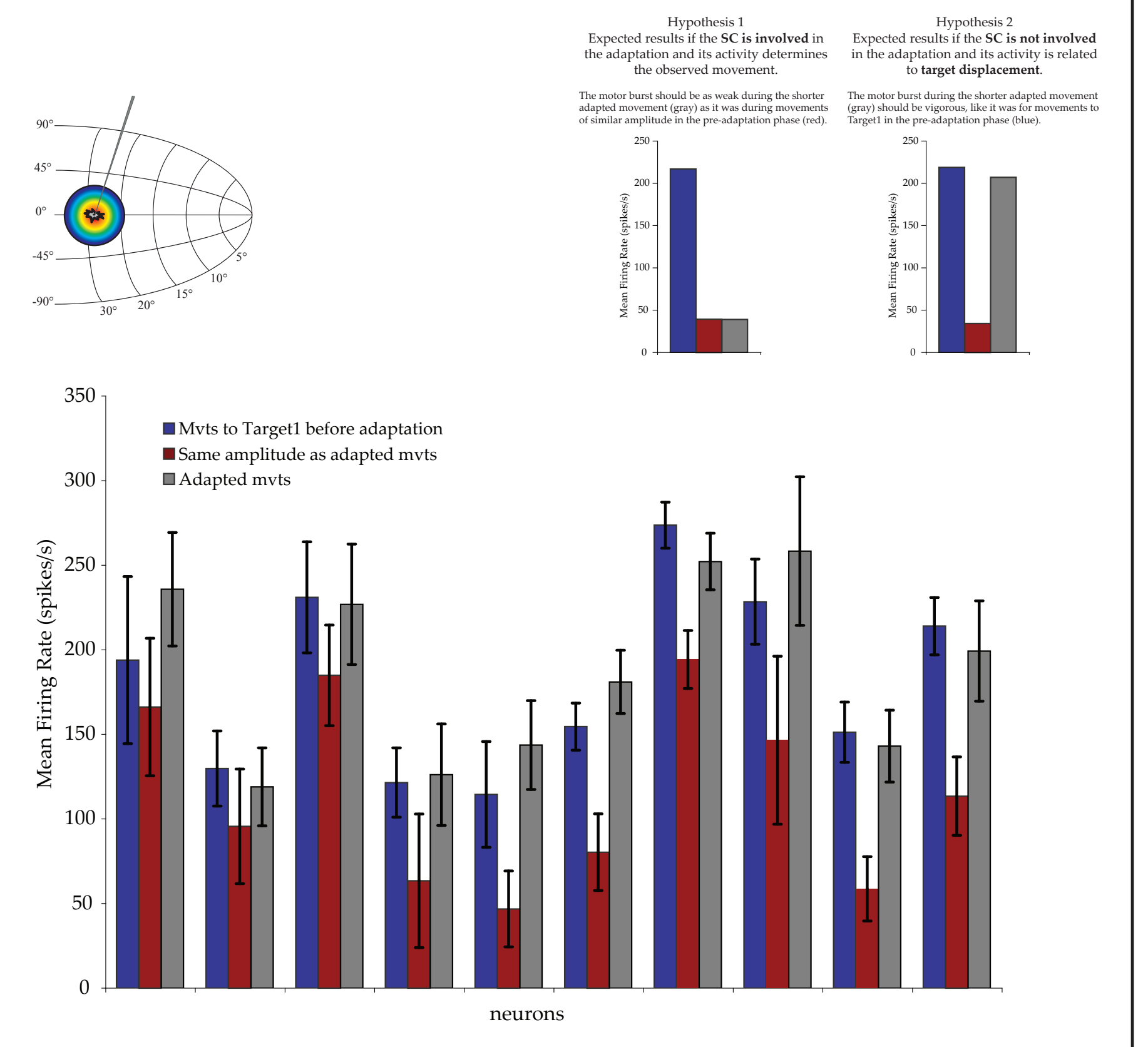

Figure 7 Mean firing rate of 10 neurons showing vigorous activity for relatively large amplitude movements (>15 degrees). The main histogram shows the activity during movements to T1 in the pre-adaptation phase (blue), during adapted movements (gray) and during movements of similar amplitude in the pre-adaptation phase (red). Target1 was placed at the center of the movement field. Upper-right inset shows the expected results according to the two main hypotheses.

Neurons' activity during adaptation toward the center of its movement field.

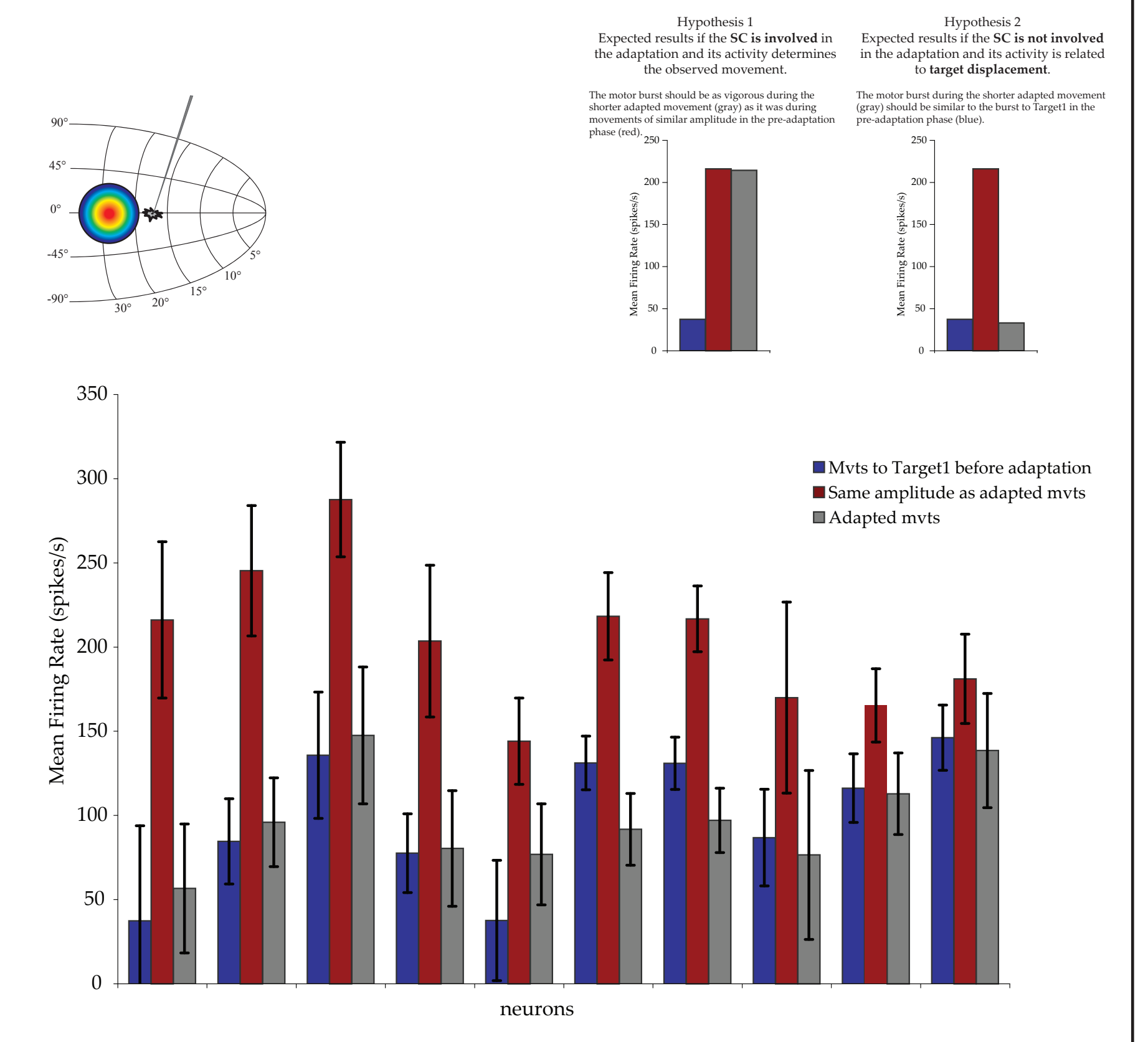

Figure 8 Mean firing rate of 10 neurons showing vigorous activity for relatively small amplitude movements (<15 degrees). The main histogram shows the activity during movements to T1 in the pre-adaptation phase (blue), during adapted movements (gray) and during movements of similar amplitude in the pre-adaptation phase (red). Target1 was placed at an eccentricity approximately 50% larger than the center of the movement field. Upper-right inset shows the expected results according to the two main hypotheses.

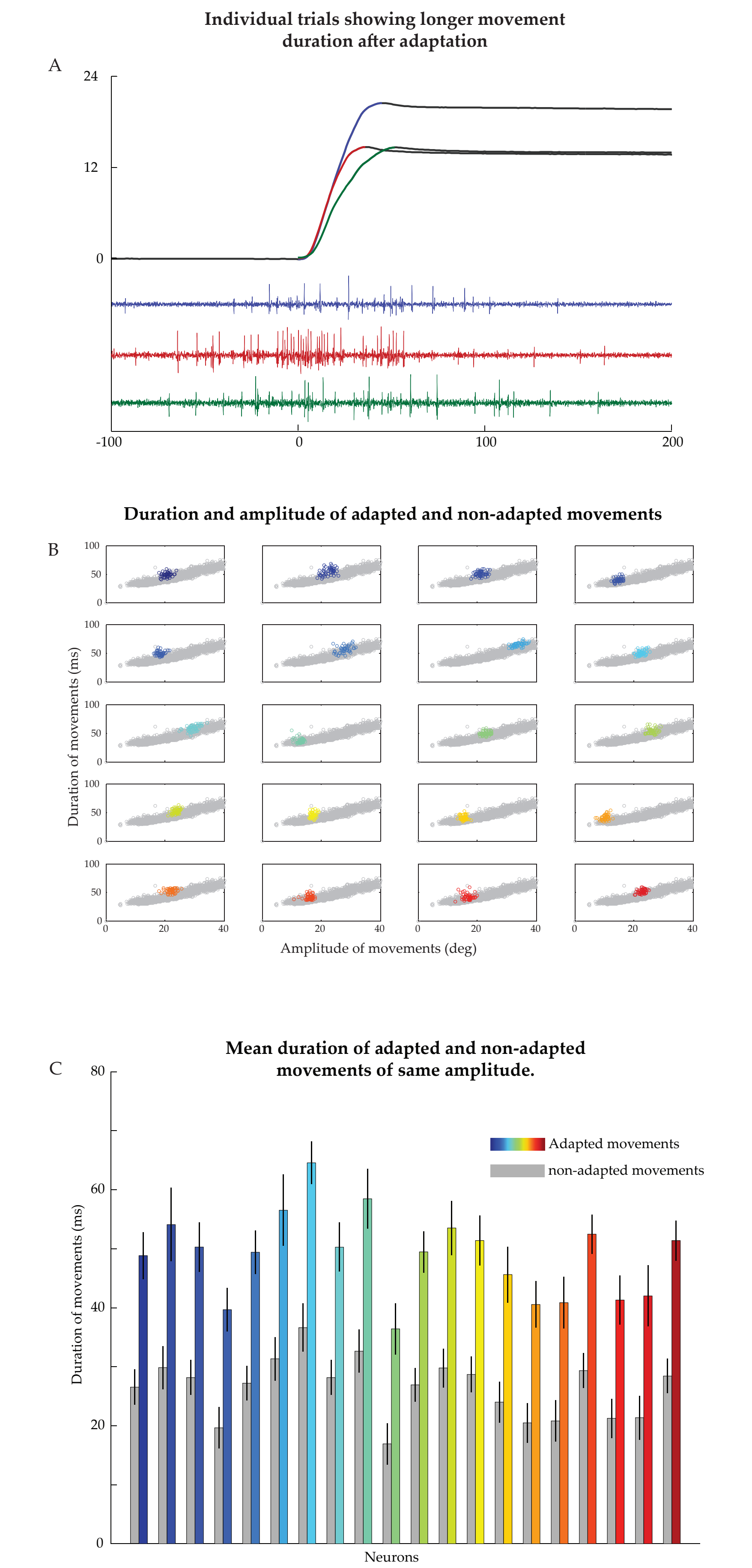

Figure 9 A- Eye movement and spike traces for large movements before adaptation (blue), short movement before adaptation (red) and short adapted movement (green). B- Relationship between the amplitude and the duration of the movements in 20 adaptation sessions. Non-adapted movements (gray) and Adapted movements (color). C- Histogram showing the mean for the same data.

Conclusions

Our results indicate that during adaptation, the activity of the neurons of the deeper layers of the Superior Colliculus represents the target displacement and not the observed movement. The motor command is characteristic of the original movement, not the adapted movement. This suggests that the Superior Colliculus is not directly involved in the mechanisms of adaptation.

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