

Do Extraocular Motoneurons Encode Head Velocity during Head-Restrained versus Head-Unrestrained Saccadic and Smooth Pursuit Movements?

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Microstimulation experiments in the superior colliculus¹ and single-unit recordings from its target, the premotor saccadic burst neurons² (SBNs, located in the paramedian pontine reticular formation), have shown that the saccadic burst generator encodes head as well as eye movements during head-unrestrained gaze shifts. There is also evidence suggesting that premotor circuits likely encode eye and head motion during head-unrestrained gaze pursuit.^{3,4} Hence, although extraocular muscle motoneurons directly drive the eye movements, the premotor inputs they receive during voluntary gaze redirection behaviors are related to eye *and* head motion. To account for this apparent mismatch in premotor/motor drives during head-unrestrained movements, two mechanisms have been envisaged: (1) a premotor signal proportional to the head contribution of the gaze shift is subtracted out at the level of the motoneurons, or (2) individual motoneurons encode eye and head motor commands, and proper eye movements result from interactions at the level of the oculomotor plant. Rather surprisingly, previous metric-based studies of extraocular motoneuron discharges during gaze shifts have suggested that the latter mechanism may be more appropriate.^{5,6} Here, we have characterized the firing rates of extraocular motoneurons in head-restrained and head-unrestrained conditions using a more sophisticated dynamic-based approach and find that metric-based analyses can yield misleading results.

As we have previously shown, the firing rates of extraocular motoneurons and internuclear neurons in the abducens nucleus (collectively referred to as ABNs) during head-restrained eye movements could be well approximated using a first-order dynamic model of eye motion.⁷ In the present study, we characterized and compared the discharge dynamics of the *same* isolated ABNs ($n = 7$, obtained from two trained rhesus monkeys) during (1) head-restrained saccades versus head-unrestrained gaze shifts, and (2) head-restrained smooth pursuit versus head-unrestrained gaze pursuit. We first observed that the activity of ABNs, in contrast to that of SBNs, remains related to the *eye* motion by the same dynamic relationship during head-restrained saccades and head-unrestrained gaze shifts.⁵ This is illustrated in FIGURE 1A (head-

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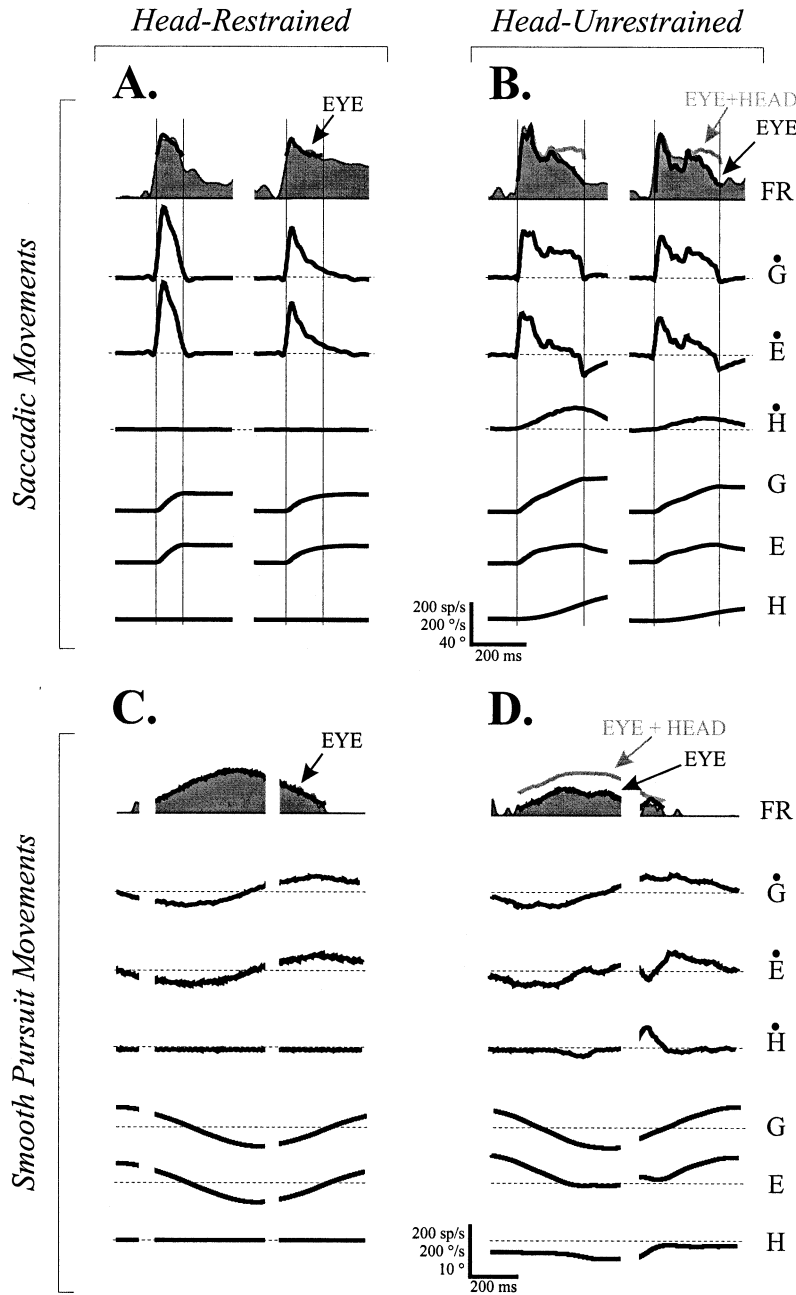


FIGURE 1. Activity of a typical ABN during head-restrained and head-unrestrained saccadic and smooth pursuit movements. (A) Model fit to head-restrained saccade-related discharges based on a simple first-order function of eye motion: $FR(t) = b + kE(t - t_d) + r\dot{E}$

restrained saccades) and 1B (head-unrestrained gaze shifts) for a typical ABN. Clearly, model predictions based on parameters estimated during saccades and that used gaze motion (gaze = eye + head) as the input tended to overestimate the neuron's firing rate during head-unrestrained gaze shifts, while predictions that used eye motion as the input provided an accurate fit. This is especially obvious toward the end of the gaze shifts, where the eye and gaze trajectories dissociated as a result of the increased head contribution.

We next extended our characterization of the same sample of ABNs to head-restrained and head-unrestrained smooth pursuit movements. FIGURE 1C and D shows the activity of our example neuron during head-restrained smooth pursuit and head-unrestrained gaze pursuit, respectively. The gaze pursuit strategy of the monkey provided a good opportunity to dissociate eye- from gaze-related discharge dynamics: while the gaze position and velocity trajectories were comparable to those of head-restrained smooth pursuit, the eye position and velocity profiles differed markedly as a result of the head contribution. Clearly, this example neuron discharged differently during head-restrained and head-unrestrained pursuit (compare FIG. 1C and D), suggesting that it did not encode gaze motion. Indeed, as was the case for gaze shifts, only the eye-based predictions could accurately describe the neuron's activity during eye-head gaze pursuit.

Our results indicate that individual ABNs encode eye movement-related signals *at all times*, therefore implying that all premotor head-related signals are offset at the level of the abducens nucleus by other premotor inputs. It has been shown that position-vestibular-pause (PVP) neurons, which mediate the vestibulo-ocular reflex, encode residual head-related information during most head-unrestrained gaze shifts.⁸ We propose that during gaze shifts the residual modulation of PVPs cancels the head-related signals carried by SBNs, such that individual motoneurons encode the eye-related signals required to move the eyeball in the orbit. Furthermore, in light of recent results from our laboratory,⁹ we also propose that the residual head-related modulation carried by PVP neurons during head-unrestrained gaze pursuit similarly functions to offset putative head-related signals carried by premotor smooth pursuit structures.

($t - t_d$), where t_d is the neuron's optimal lead time, and b , k , and r are constant model parameters. The mean variance accounted for obtained across our sample of neurons ($\overline{\text{VAF}}$) using this model was 0.66 ± 0.15 . The thin vertical lines denote the onset and offset of the saccades ($20^\circ/\text{s}$ criterion), and the horizontal dashed lines mark zero velocity (and zero position when applicable). (B) Model predictions for the same neuron during head-unrestrained gaze shifts obtained using the parameters estimated in A and either eye motion (black curve; $\overline{\text{VAF}} = 0.37 \pm 0.24$) or gaze motion (gray curve; $\overline{\text{VAF}} = -0.48 \pm 0.75$) as the model input. Panels A and B were modified from Cullen *et al.*⁵ (C) First-order model fit to the same neuron's discharge during head-restrained smooth pursuit ($\overline{\text{VAF}} = 0.75 \pm 0.15$). Note that the estimated parameters b , k , and r differed significantly from those estimated during saccades.⁷ (D) Model predictions for the same neuron during head-unrestrained gaze pursuit using the parameters estimated in C and when the input was either eye motion (black curve; $\overline{\text{VAF}} = 0.54 \pm 0.21$) or gaze motion (gray curve; $\overline{\text{VAF}} = 0.11 \pm 0.30$). Abbreviations: FR, firing rate; G, E, and H, gaze, eye, and head velocity; G, E, and H, gaze, eye, and head position.

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