

# Passive Activation of Neck Proprioceptive Inputs Does Not Influence the Discharge Patterns of Vestibular Nuclei Neurons

JEFFERSON E. ROY AND KATHLEEN E. CULLEN

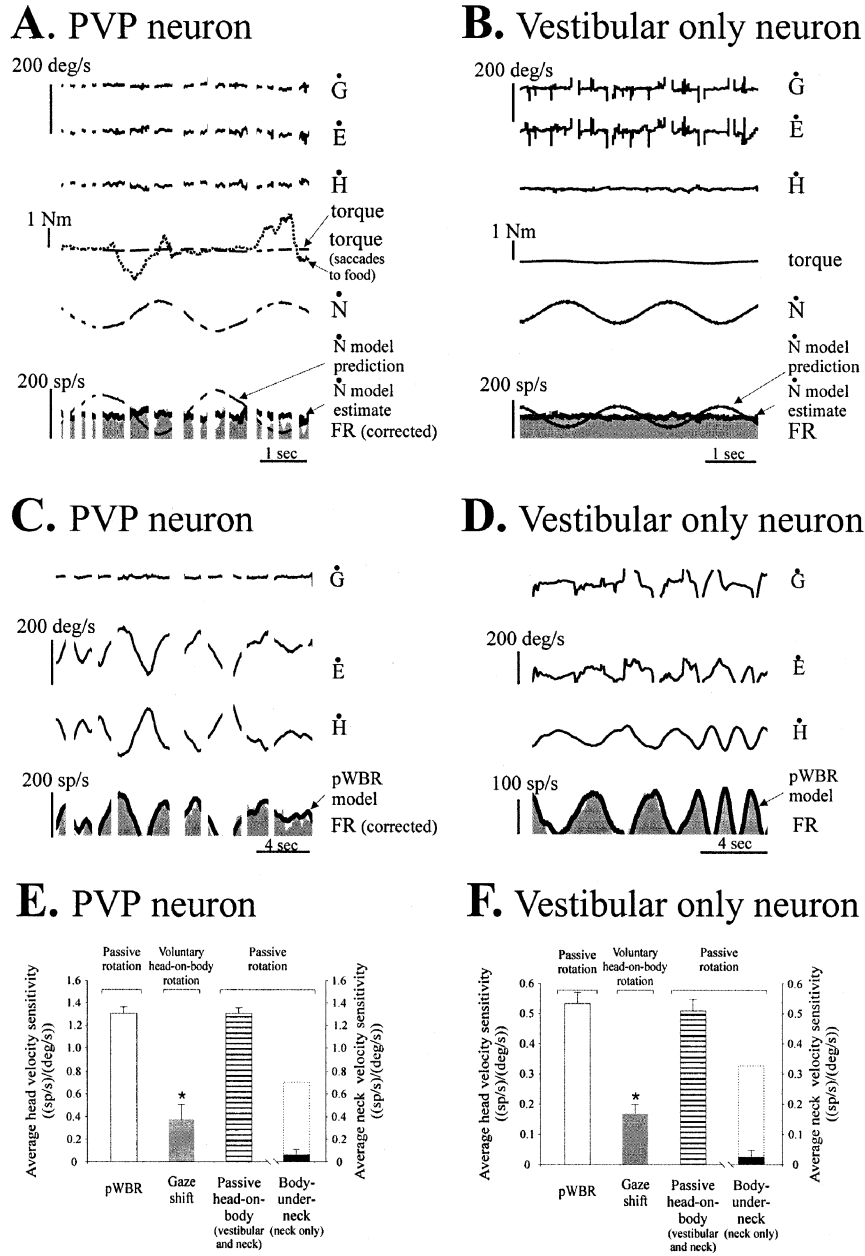
*Aerospace Medical Research Unit, Department of Physiology,  
McGill University, Montreal, Quebec, H3G 1Y6 Canada*

Position-vestibular-pause (PVP) neurons and vestibular only (VO) neurons are thought to mediate the vestibulo-ocular and vestibulo-collic reflexes, respectively. Both neuron classes are much less sensitive to head motion during *active* gaze shifts than during *passive* whole-body rotation (pWBR).<sup>1-5</sup> The mechanism that underlies this differential processing of vestibular information is not known. Neck muscle proprioceptive inputs have been proposed to contribute to the observed attenuation. While experiments in decerebrate animals have shown that neck proprioception can modulate the responses of vestibular neurons,<sup>6,7</sup> studies in alert monkeys have reported varying degrees of influence.<sup>3,8-10</sup> However, these latter studies assumed that the monkey did not generate a neck motor command during the paradigms used to evaluate neck proprioceptive inputs. Since a coincident neck efference command could effect neuron discharges, in this study we measured the torque produced during passive rotation of the body relative to a stationary head, thereby allowing us to dissociate the effect of neck proprioception from efference commands.

The discharge activity of vestibular neurons in three rhesus monkeys was initially recorded during voluntary eye movements and pWBR with the monkeys in the head-restrained condition. After a neuron was fully characterized, the monkey's head was slowly and carefully released, allowing free rotation of its head through its natural range of motion. The response of the same neuron was then recorded during the voluntary head movements made during combined eye-head gaze shifts (15° to 65°). In agreement with previous studies, the head velocity sensitivities of PVP ( $n = 17$ ) and VO ( $n = 40$ ) neurons were significantly attenuated during gaze shifts as compared to those estimated during pWBR (mean sensitivity ( $\pm$  SEM) =  $0.37 \pm 0.17$  vs.  $1.31 \pm 0.13$  (spk/s)/(deg/s), and  $0.17 \pm 0.03$  vs.  $0.53 \pm 0.04$  (spk/s)/(deg/s), for PVP and VO neurons, respectively; FIG. 1E and F, compare white and gray-shaded columns).

The influence of neck proprioceptive inputs on vestibular neurons was first tested by passively rotating the monkeys' bodies while their heads were held earth-station-

Address for correspondence: Dr. Kathleen E. Cullen, Department of Physiology, McGill University, 3655 Drummond St., Room 1220, Montreal, Quebec, H3G 1Y6. Tel: (514) 398-5709; fax: (514) 398-8241.  
cullen@med.mcgill.ca



**FIGURE 1.** Activity of typical PVP and VO neurons during passive activation of neck proprioceptive inputs. Both PVP (A) and VO (B) neurons were unresponsive to the passive rotation of the neck when the head was held earth-stationary ( $\dot{N}$  model estimate, heavy trace). The neural activity of PVP (C) and VO (D) neurons was well predicted during pas-

ary. The torque generated during this paradigm was consistently small ( $< \pm 0.4$  Nm; FIG. 1A and B) compared to when head-restrained monkeys oriented to food targets ( $> \pm 3.5$  Nm; FIG. 1A, dotted trace), indicating that the monkey was generating a minimal voluntary neck command. A model based on the predicted neck velocity sensitivity necessary to fully suppress the head velocity-related activity of the neurons during gaze shifts overpredicted the discharges of the neurons (FIG. 1A and B, model prediction, thin trace). Neuronal activity was well described by the spontaneous discharge rates of the PVP and VO neurons (FIG. 1A and B, model estimate, heavy trace). Indeed, the estimated modulation of PVP ( $n = 7$ ) and VO ( $n = 15$ ) neurons in response to the passive neck rotation was negligible (mean sensitivity =  $0.06 \pm 0.2$  and  $0.09 \pm 0.1$  (spk/s)/(deg/s), respectively; FIG. 1, E and F, solid columns, respectively), which suggests that neck afferent activation does significantly contribute to the attenuation that was observed during gaze shifts.

We next characterized the influence of neck afferent inputs by rotating the monkeys' heads passively on their earth-stationary bodies, eliciting head-on-body movement trajectories and velocities similar to those generated during large gaze shifts (mean head velocity =  $192 \pm 66$  vs.  $165 \pm 55$  deg/s for  $55^\circ$ – $65^\circ$  gaze shifts). Neural discharges of both PVP ( $n = 9$ ) and VO ( $n = 23$ ) neurons were well predicted by a model based on the head velocity sensitivity during pWBR (FIG. 1C and D, pWBR model, heavy trace). Indeed, the estimated head velocity sensitivities of PVP and VO neurons showed little attenuation relative to passive WBR (mean sensitivity =  $1.30 \pm 0.19$  and  $0.51 \pm 0.04$  (spk/s)/(deg/s); FIG. 1E and F, horizontally stripped columns, respectively), indicating that the passive activation of the neck proprioceptors did not alter the sensitivity of the neurons to head-in-space motion.

Our results indicate that passive activation of neck afferent inputs does not significantly influence the discharge activity of vestibular neurons when voluntary commands to the neck muscles are minimal. We suggest that other mechanisms, most likely efferent copies of the gaze and neck motor commands, are responsible for the differential processing of vestibular information during gaze shifts.

#### ACKNOWLEDGMENTS

This study was supported by the CIHR and the FRSQ.

---

sive rotations of the monkey's head on its stationary body by a model based on the head velocity sensitivity of the neurons during pWBR (pWBR model). (E,F) PVP and VO neurons had reduced sensitivity to head velocities generated during gaze shifts (*gray-shaded columns*) as compared to pWBR (*open columns*). The negligible neck velocity sensitivity (*solid columns*) and the unaltered head velocity sensitivity during passive head-on-body rotations (*horizontally stripped columns*) indicate that a neck afferent input is not the mechanism responsible for these attenuated responses. A much greater neck velocity sensitivity would be necessary to account for the observed attenuation (*dashed line columns*). Note: firing rates of PVP neurons have been corrected for their eye position sensitivities. Traces directed upwards are in the ipsilateral direction. Error bars show SEM. E: eye-in-head velocity;  $\dot{H}$ : head velocity;  $\dot{G}$ : gaze velocity (=  $\dot{E} + \dot{H}$ );  $\dot{N}$ : neck velocity; FR: firing rate.

## REFERENCES

1. BOYLE, R., T. BELTON & R.A. MCCREA. 1996. *Ann. N.Y. Acad. Sci.* **781**: 244–263.
2. MCCREA, R.A., C. CHEN-HUANG, T. BELTON & G.T. GDOWSKI. 1996. *Ann. N.Y. Acad. Sci.* **781**: 292–303.
3. MCCREA, R.A., G.T. GDOWSKI, R. BOYLE & T. BELTON. 1999. *J. Neurophysiol.* **82**: 416–428.
4. ROY, J.E. & K.E. CULLEN. 1998. *Nature Neurosci.* **1**: 404–410.
5. ROY, J.E. & K.E. CULLEN. 1999. *Soc. Neurosci. Abstr.* **25**: 265.
6. BOYLE, R. & O. POMPEIANO. 1981. *J. Neurophysiol.* **44**: 633–649.
7. ANASTASOPOULOS, D. & T. MERGNER. 1982. *Exp. Brain Res.* **46**: 269–280.
8. GDOWSKI, G.T. & R.A. MCCREA. 1999. *J. Neurophysiol.* **81**: 436–449.
9. KHALSA, S.B., R.D. TOMLINSON, D.W. SCHWARZ & J.P. LANDOLT. 1987. *J. Neurophysiol.* **57**: 1484–1497.
10. KHALSA, S.B., R.D. TOMLINSON & D.W. SCHARWZ. 1988. *Acta Otolaryngol.* **106**: 269–275.