NIH Public Access
Author Manuscript
Trends Cogn Sci. Author manuscript; available in PMC 2015 February 01.

Published in final edited form as:
Trends Cogn Sci. 2014 February ; 18(2): 66–67. doi:10.1016/j.tics.2013.10.015.

Cerebellum estimates the sensory state of the body

David J. Herzfeld and **Reza Shadmehr**
Department of Biomedical Engineering, Laboratory for Computational Motor Control, Johns Hopkins University School of Medicine, Baltimore, MD 21205, USA

Abstract

A recent neurophysiology study provides data from the cerebellar vermis/nodulus, where neurons encode translation of the head, even when these translations are induced via an illusion. These data provide new neurophysiological evidence that the cerebellum is important for computations involving internal models of motion, estimating the state of the body.

Deep inside your smart phone, you have an accelerometer and a gyroscope. The accelerometer reports a vector: the sum of linear acceleration caused by movements of your phone and the gravity vector. The gyroscope reports the rate of rotation of this vector. Together, these two sensors are used by the phone's software to estimate its orientation with respect to gravity. However, despite the sophistication of these sensors, your phone is poor at estimating linear motion. That is, it cannot tell you with much accuracy that you just picked it up and placed it 10cm to the right. Why? Because acceleration is a vector that is the sum of two components, and when you move your phone, it would have to know the vector of gravity before it could estimate the vector due to linear motion. Your brain, however, can solve the same problem with exquisite accuracy. When you are in a car and press on the accelerator, the net acceleration vector is tilting away from gravity, but you do not perceive this as a tilting of your head. Rather, your brain is able to accurately perceive the linear motion because you have vision and other sensors that allow you to accurately estimate the direction of gravity. Therefore, you perceive the tilting of the acceleration vector as linear motion. What your brain does very well, and the smart-phone does poorly, is called state-estimation.

How is it that the brain can perform accurate state-estimation? A prominent theory is that it accomplishes this feat because in the cerebellum, there is special machinery that incorporates the various sensors, and efference copy, to provide an estimate of state of the head. These sensors include vestibular information supplied via primary otolith afferents (measurement of acceleration), afferents from the semicircular canals (head's rotation), and vision. In a recent paper, Jean Laurens and colleagues [1] tested this idea by inducing an illusion, making the animal feel as though its head was translating, when in fact it had been rotated. They found that activity in the Purkinje cells reported the translation, demonstrating that the cerebellar cortex uses its various inputs to produce an estimate of the state of the body.

© 2013 Elsevier Ltd. All rights reserved.

Correspondence: Reza Shadmehr, 410 Traylor Building, Johns Hopkins School of Medicine, 720 Rutland Ave, Baltimore, MD 21205, USA, shadmehr@jhu.edu.

Publisher's Disclaimer: This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

NIH-PA Author Manuscript
NIH-PA Author Manuscript
NIH-PA Author Manuscript

NIH-PA Author Manuscript
NIH-PA Author Manuscript
NIH-PA Author Manuscript

To induce this illusion, Laurens et al. [1] relied on the fact that the outputs of the semicircular canals decay during continuous rotation. If the head is tilted during this period, acceleration signals measured by the otoliths do not correspond to the motion signals measured by the canals. The difference is perceived as a combination of tilt and translational acceleration (the tilt while rotating effect, TWR). Behavioral correlates of this false translation signal have been measured in both humans and monkeys using the vestibular ocular reflex (VOR) [2,3]. Laurens et al. [1] recorded from Purkinje (P) cells in the nodulus and uvula of the cerebellum whose responses were modulated only by translational accelerations. During TWR, these cells showed responses consistent with the illusionary translational signals. The results demonstrated that linear acceleration was computed using a combination of signals from at least the otoliths and semicircular canals rather than simply using a transformation of one of the signals independently, and cerebellar cortex activity reflected the result of these computations (although the extent to which these computations actually take place in the cerebellum is not clear).

The authors propose that the P-cell activity in the cerebellum reflects the output of a forward model that tracks the direction of gravity vector over time. A forward model is a computation that does the following: given the past estimate of sensory state, current sensory measurements, and efference copy, it predicts the current sensory state [4]. The illusion, in this case, arises because the otoliths high-pass filter the rotation signals, which in turn provides the forward model the sensory measurements that result in a state-estimate that implies head translation.

Neural calculations that involve multiple sensory modalities (i.e. multi-sensory integration) cannot, by themselves, be described as a forward model; more evidence is required. The authors provide an interesting approach – using a computational model, they predict the neurophysiological properties of the P-cell and behavioral VOR on a monkey-specific basis. That is, the authors recorded from three different monkeys, each with different physical properties. The authors show that differences in the responses of different monkeys were predicted by differences in the physical dynamics of the animals.

Does the cerebellum possess the machinery necessary to carry out this forward model computation? This question cannot be answered by observing Purkinje-cell firing rates because the actual computations may be carried out elsewhere, and provided as input to the cerebellum. However, lesion results provide evidence that the cerebellum may be at least a necessary node for this computation [5]. When the nodulus and uvula are surgically removed, the VOR is no longer consistent with the actual state of the head, indicating that integration of rotation and acceleration signals to track head position does not occur. Therefore, the cerebellum appears to be a necessary structure to integrate the information from the otolith and canal afferents to provide state-estimation, as reflected in the activity of P-cells.

Sensory illusions are a powerful method to test for the neural basis of forward models. For example, when people use a manipulandum to move a cursor on the screen, the geometric relationship between the motion of the hand and the motion of the cursor can be altered. After people learn the new relationship, they form an illusion regarding the motion of their own hand. Interestingly, people with cerebellar damage can also learn this relationship, but do not form the illusion [6], providing further evidence that the cerebellum may be critical for encoding of forward models.

In summary, Laurens et al. [1] provide new evidence that translational-selective neurons in lobules IX/X of the cerebellum estimate the state of the head using a computation that is consistent with a forward model.

NIH-PA Author Manuscript
NIH-PA Author Manuscript
NIH-PA Author Manuscript

Reference list

1. Laurens J, et al. Computation of linear acceleration through an internal model in the macaque cerebellum. Nature Neuroscience. 2013
2. Merfeld DM, et al. Humans use internal models to estimate gravity and linear acceleration. Nature. 1999; 398:615–618. [PubMed: 10217143]
3. Laurens J, et al. Processing of angular motion and gravity information through an internal model. Journal of Neurophysiology. 2010; 104:1370–1381. [PubMed: 20610780]
4. Wolpert DM, Miall RC. Forward Models for Physiological Motor Control. Neural Networks. 1996; 9:1265–1279. [PubMed: 12662535]
5. Angelaki DE, Hess BJ. Lesion of the nodulus and ventral uvula abolish steady-state off-vertical axis otolith response. Journal of Neurophysiology. 1995; 73:1716–1720. [PubMed: 7643178]
6. Izawa J, Criscimagna-Hemminger SE, Shadmehr R. Cerebellar contributions to reach adaptation and learning sensory consequences of action. Journal of Neuroscience. 2012; 32:4230–4239. [PubMed: 22442085]