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Cerebellum estimates the sensory state of the body

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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 smartphone, 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 10 cm 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 accurately to 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 smartphone 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 (the head's rotation), and vision. In a recent paper, Jean Laurens and colleagues [1] tested this idea by inducing an illusion: making an animal feel as though its head were translating, when in fact it had been rotated. They found that activity in the Purkinje (P) cells reported the translation, demonstrating that the cerebellar cortex uses its various inputs to produce an estimate of the state of the body.

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 [TWR] effect). 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 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 occur in the cerebellum is unclear).

The authors propose that the P-cell activity in the cerebellum reflects the output of a forward model that tracks the direction of the 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 with the sensory measurements that result in a state estimate that implies head translation.

Neural calculations that involve multiple sensory modalities (i.e., multisensory 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 perform this forward-model computation? This question cannot be answered by observing P-cell firing rates because

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the computations may be conducted 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 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 the 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 the encoding of forward models.

In summary, Laurens *et al.* [1] provide new evidence that translation-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.

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An exemplar of model-based cognitive neuroscience

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Are categories learned by forming abstract prototypes or by remembering specific exemplars? Mack, Preston, and Love observed that patterns of functional MRI (fMRI) brain activity were more consistent with patterns of representations predicted by exemplar models than by prototype models. Their work represents the theoretical power of emerging approaches to model-based cognitive neuroscience.

A primary aim of cognitive science is to understand the mechanisms that give rise to faculties of mind like perception, learning, and decision making. One approach formalizes hypotheses about cognitive mechanisms in computational models. Cognitive models predict behavior, like the errors people make and the time it takes them to respond, and how behavior varies under different conditions, using different stimuli, with different amounts of learning. Another approach turns to the brain to identify neural mechanisms associated with different aspects of cognition, using techniques like neurophysiology, electrophysiology, and fMRI.

These two come together in a powerful new approach called model-based cognitive neuroscience [1]. Cognitive models decompose complex behavior into representations and processes and these latent model states are used to explain the modulation of brain states under different experimental conditions. Reciprocally, neural measures provide additional data that help constrain cognitive models and adjudicate between competing cognitive models that make similar predictions of behavior. For example, brain measures are related to cognitive model parameters fitted to individual participant data [2], measures of brain dynamics are related to measures of model dynamics [3,4], model parameters are constrained by neural measures [4], model parameters are used in statistical analyses of neural data [5], or neural data, behavioral data, and cognitive models are analyzed jointly within a hierarchical statistical framework [6].

Mack, Love, and Preston [7] adopted a model-based cognitive neuroscience approach to understand the mechanisms involved in category learning [8]. Consider everyday categories like dogs, cars, or chairs. Categories like these are abstractions in the sense that collections of visibly different objects are treated as the same kind of thing. But does that imply that the mental representations of categories are inherently abstract and that category learning involves creating abstractions? The earliest work on categorization assumed abstraction, either in the form of logical rules defining category membership or in the form of abstract prototypes capturing the family resemblance of category members. However, later work showed that cognitive models based on memory for experienced category exemplars could predict experimental results

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