nature neuroscience

Estimating the sources of motor errors for adaptation and generalization

Max Berniker[1,2] & Konrad Kording[1,2]

Motor adaptation is usually defined as the process by which our nervous system produces accurate movements while the properties of our bodies and our environment continuously change. Many experimental and theoretical studies have characterized this process by assuming that the nervous system uses internal models to compensate for motor errors. Here we extend these approaches and construct a probabilistic model that not only compensates for motor errors but estimates the sources of these errors. These estimates dictate how the nervous system should generalize. For example, estimated changes of limb properties will affect movements across the workspace but not movements with the other limb. We provide evidence that many movement-generalization phenomena emerge from a strategy by which the nervous system estimates the sources of our motor errors.

Suppose I throw a stone with my right hand and it travels less than I had expected. This observation can have at least two interpretations: the stone may be heavier than I thought, or my arm may be weaker than I thought. If I believe the stone to be heavier, I will adjust accordingly the next time I throw the same stone, with my right or my left arm. Movements I make without the stone, clearly, shouldn't be influenced by my updated estimate of the stone's weight. If, on the other hand, I believe my right arm to be weaker, I will adjust future movements with this arm, with or without the stone, but not subsequent movements of my (unaffected) left arm. This example highlights what our intuition suggests and dynamics demands: the nervous system needs to estimate not only the necessary corrections (for example, throw with more effort) but also the sources of errors (for example, the stone is heavy or my arm is weak) when we adapt our movements.

Ideally, the nervous system should treat the body and the world as a coupled dynamical system whose properties constantly change over time. For instance, the strength of each of our muscles may vary over time (through fatigue, exercise, injury, aging and so forth). Similarly, the objects we interact with have variable properties and dynamics. To adapt and generalize, the nervous system needs to attribute observed movement errors to either the body or the world and then estimate the value of those properties.

Many studies have analyzed how human subjects adapt to perturbations and have found that they estimate these disturbances instead of simply memorizing a motor plan[1,2]. This idea is captured by the notion of an internal model, a representation of how our motor system predicts the outcome of motor commands. Studies that examine internal models assume that motor errors, regardless of their source, are estimated with a general model of disturbances. Although some studies do recognize that multiple sources may be responsible for motor errors[3,4], their internal models do not distinguish between them. This single model compensates for any changes in the properties of the world or the body. As a result, these models have no mechanism for representing that an estimated change in the limb should generalize across the workspace but not to the other limb, and that an estimated change in the world should generalize to the other hand.

Here we present a model that formalizes the estimation of the sources of motor errors by adapting its representation of both the body and the world. This source-estimation model constantly updates its parameter estimates and its uncertainty about those estimates through an application of bayesian inference. To test the model, we compare its predictions to three classes of published motor adaptation studies: velocity-dependent force fields, rotating (Coriolis) rooms and inertial perturbations. Our model predicts many findings of these experiments. These results support our hypothesis that the nervous system adapts and generalizes by estimating the sources of motor errors.

RESULTS

Modeling sources of errors: body and world

As in the example of throwing a stone, a continuum of possible parameter values can explain many motor errors equally. In addition, owing to noisy perception and commands, the motor system operates under uncertain conditions. The nervous system therefore needs to assign credit to the likely parameters and estimate their properties. Bayesian inference is a systematic method for optimally solving such a credit-assignment problem. For example, if we knew the stone's weight with great certainty and errors in our estimate of its inertia could not account for the motor errors we observed, then other sources, such as limb properties, would be considered likely culprits. This would result in relatively small changes in our estimate of the stone's weight and large changes in our estimates of limb properties (for example, mass,

[1]Rehabilitation Institute of Chicago, Department of Physical Medicine and Rehabilitation, Northwestern University, 345 E. Superior Street, ONT-931, Chicago, Illinois 60611, USA. [2]These authors contributed equally to this work. Correspondence should be addressed to M.B. (mbernike@northwestern.edu).

Received 19 August; accepted 21 October; published online 16 November 2008; doi:10.1038/nn.2229