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Looking for synergies between the equilibrium point hypothesis and internal models

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The nervous system needs to control movement of a complex body in a complex world subject to uncertainty due to sensory and motor noise. In this issue, Mark Latash argues in favor of a framework that addresses these problems – the Hierarchical Equilibrium Point Hypothesis (as we call it here, HEPH). According to this hypothesis, movement is created by having a central controller specify a shift in the reference body configuration. This time-varying reference body configuration is passed on to lower level (e.g., limb) controllers, and finally to the lowest level controllers which set the thresholds of the tonic stretch reflex of individual muscles as assumed in the lambda model.

In the context of this paper we find it useful to discuss other approaches, in particular approaches that focus on estimation (e.g. Internal models, IMs) and approaches that focus on control given estimations (e.g. Optimal control, OC)¹. Specific proposals have been put forward of how the nervous system may implement estimation (*neural* IM) and proposals of how the nervous system may implement control (*neural* Control, nC). The EPH is a version of nC which suggests that the motor system simplifies the control problem by centrally adjusting parameters of the spinal proprioceptive feedback. The idea of distributed hierarchical control seems to have emerged in many communities to solve the problem of control complexity. We will briefly review the differences across approaches and highlight possible synergies.

Computational goals in the frameworks

Uncertainty in the state of the body and properties of external environment is recognized as one of the central problems in motor control. Even when the environment is predictable (e.g. force fields in typical IM studies), uncertainty remains due to, e.g., sensory and motor noise. It seems that most nC studies including those of the EPH and the nIM flavor focus on different possible neural mechanisms of control of movement that deal with uncertainty in distinct ways. EPH studies have mostly involved well learned tasks in predictable environments, and assumed that the spinal proprioceptive *feedback* is sufficient to minimize errors due to uncertainty. In contrast, many nIM studies focus on the minimization of errors

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¹In the context of this paper, we define OC as a model that only asks about the nature of the computational objective and that derives the best possible solution. We define IM as a model (forward or inverse) that specifies which algorithm is used by the nervous system to make predictions.

due to uncertainty by *prediction* or feedback. The IM and OC frameworks aim at developing computational methods to understand how the nervous system generates predictions and combines them with feedback for the control of movement.

One issue where EPH disagrees with most other frameworks is the complexity of the central control. According to the Feldman and Latash version of EPH, the central controller generates a relatively simple equilibrium trajectory while the spinal proprioceptive feedback deals with the dynamics of the task and noise thus rendering prediction about the dynamics of the task unnecessary. According to some IM and OC ideas, the nervous system is so powerful that it can control optimal forces for every muscle. It seems that the nervous system relies on predictions as well as muscle mechanics and spinal feedback to simplify control, and it is only a question of degree how detailed the predictions of the nervous system are and how much it relies on peripheral feedback.

Control Hierarchy

At the heart of the target article is the notion of a hierarchical organization of control. The origins of this idea in motor control go back at least to Bernstein (1967) and the theoretical studies of complex systems by Gelfand and Tsetlin (Gelfand & Tsetlin, 1962). In HEPH, a controller at each level of the hierarchy maps a small number of input variables to many output (elemental) variables and thus imposes co-variations (synergies) between the elemental variables. What is missing in the current HEPH framework is a specific description of the structure of the hierarchical controllers and an algorithm of how to obtain these controllers.

OC directly predicts synergies in tasks in which some dimensions are more important than others (Lockhart & Ting, 2007; Todorov & Jordan, 2002) and it does allow specifying how controllers could be obtained and learned. With respect to hierarchies, it was found that many reinforcement learning problems can be solved more efficiently by assuming a hierarchical representation (Dayan & Hinton, 1993; Dietterich, 1999). Such solutions are attractive as they can naturally deal with the distributed representations inherent in the nervous system (Haruno, 2003). Furthermore, OC also allows setting arbitrary constraints, for example a constraint that the controller must be hierarchical. A recent work (Todorov E, 2005) has divided control into two modules, one supposedly implemented in the spinal cord which affords a fast feedback loop and another in the brain which allows for complex predictions and planning. As such, it would seem that OC can complement the ideas voiced in the target article. For example, one might ask which hierarchical controller would generate time varying equilibrium trajectories that, on average, lead to minimal expected effort and maximally stable movement.

Some ideas of the EPH, IM, and OC frameworks could be combined for hierarchical control. If one assumes that the hierarchy has more than two levels, i.e., a spinal cord controller and multiple higher levels, then not all levels have to deal with prediction of all variables. If an input to a high level consists of abstract task variables, e.g., a desired final position and movement speed, then the output variables may be described in terms of the reference body configurations as suggested by Latash. At this level, the controller does not have to be

concerned with the dynamics of the movement. Such predictions could be handled by lower level controllers using IMs. Thus, certain ideas in these frameworks may not be contradictory if applied to the different levels of control hierarchy.

Each framework within motor control tends to focus on different aspects of motor control. EPH studies are concerned with the physiological implementation of central variables and simplicity of control afforded by the proprioceptive feedback and viscous-elastic properties of activated muscle. IM studies ask about the nature of prediction and its physiological implementation. OC combines feedback and prediction and provides computational and conceptual tools. All three frameworks aim at understanding of how the nervous system controls movements of a complex body in an uncertain world. As such, it seems that these three frameworks are complementary and can benefit from mutual interactions.

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