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COMMENTARIES

Should the Equilibrium Point Hypothesis (EPH) be Considered a Scientific Theory?

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The purpose of this commentary is to discuss factors that limit consideration of the equilibrium point hypothesis as a scientific theory. The EPH describes control of motor neuron threshold through the variable lambda, which corresponds to a unique referent configuration for a muscle, joint, or combination of joints. One of the most compelling features of the equilibrium point hypothesis is the integration of posture and movement control into a single mechanism. While the essential core of the hypothesis is based upon spinal circuitry interacting with peripheral mechanics, the proponents have extended the theory to include the higher-level processes that generate lambda, and in doing so, imposed an injunction against the supraspinal nervous system modeling, computing, or predicting dynamics. This limitation contradicts evidence that humans take account of body and environmental dynamics in motor selection, motor control, and motor adaptation processes. A number of unresolved limitations to the EPH have been debated in the literature for many years, including whether muscle resistance to displacement, measured during movement, is adequate to support this form of control, violations in equifinality predictions, spinal circuits that alter the proposed invariant characteristic for muscles, and limitations in the description of how the complexity of spinal circuitry might be integrated to yield a unique and stable equilibrium position for a given motor neuron threshold. In addition, an important empirical limitation of EPH is the measurement of the invariant characteristic, which needs to be done under a constant central state. While there is no question that the EPH is an elegant and generative hypothesis for motor control research, the claim that this hypothesis has reached the status of a scientific theory is premature.

Keywords: motor control, neural control of movement

In the target article, the author states, “There is only one coherent physical (physiological) theory that tries to identify the laws of physics that account for the neural control of biological movement.” While the equilibrium point hypothesis has played an important role in the science of motor control, it remains largely speculative, and cannot be considered a “scientific theory” because of substantial limitations in both its scope and because of controversial and largely unsupported features of the hypothesis. The definition of scientific theory published by AAAS

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is “a well-substantiated explanation of some aspect of the natural world that can incorporate facts, laws, inferences, and tested hypotheses... In science, theories do not turn into facts through the accumulation of evidence... [Theories] incorporate a large body of scientific facts, laws, tested hypotheses, and logical inferences” (2007). It is important to emphasize that scientific theories are inductive in nature and aim for predictive and explanatory force. Therefore, I consider the author’s premise overly ambitious for the EP hypothesis of motor control. The purpose of the following discussion is not to critique the validity of the Equilibrium Point Hypothesis (EPH), but rather to discuss some limitations to its consideration as a scientific theory, particularly in its predictive and explanatory power.

While the EPH may, at first glance, seem appropriate to the description of scientific theory given above, there are many factors that prevent EPH from realizing the required predictive and explanatory power. EPH is an elegant hypothesis that combines the physical behavior of the musculoskeletal system with selected but limited elements of spinal anatomy and physiology. Those elements focus heavily on the reflex circuits associated with the muscle spindle, specifically those involving the intrafusal fibers that transduce small changes in muscle length. Together with the short and long loop components of the stretch reflex, this feedback has the potential to influence muscle activation, depending on the state of the specific motor neurons that receive input, either directly or indirectly from muscle afferents. According to the EPH, motor neuron threshold is specified through descending commands, and corresponds to a unique muscle length, for a given mechanical condition in the environment. This variable is referred to as Lambda. Because of the hypothesized invariant relationship between muscle force and muscle length across the full physiological range of the muscle, a unique referent configuration can be specified by lambda, while the actual configuration depends also on external forces. Therefore, neural control of movement can be simplified to specification of this threshold-determining variable. One of the most compelling features of the equilibrium point hypothesis is the integration of posture and movement control into a single mechanism. Thus, at the end of motion and in the absence of external forces, a new posture is achieved without persistent muscle activity. Such behavior is best explained by a mechanism which modifies a position-dependent threshold, such as proposed by the EPH.

The EPH was introduced in a seminal series of papers by Feldman and colleagues (Asatrian & Fel’dman, 1965, Fel’dman, 1966a,b), which demonstrated that the force developed by a muscle, when the subject is instructed to maintain a particular angle, is a function of the length of the muscle and the variable lambda. Lambda reflected an empirically derived value, the minimum length at which the passively lengthened muscle begins to be excited when the subject is asked not to intervene. These papers introduced the concept of an invariant characteristic for the muscle, or the force/length relationship for a given instructed state, presumably reflecting the centrally specified value, lambda. Further, these early papers generalized the concept from a muscle to a group of muscles acting about a joint. Later studies generalized the model to multiple joints (Flash, 1987), and whole body postures as well as to locomotor control (Feldman et al., 2011).

From a neuroanatomical perspective, the equilibrium point hypothesis has two essential levels of consideration: spinal circuitry that provides the basis for lambda as a control variable, and supraspinal processes that generate lambda. While the

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essential core of the hypothesis is based upon spinal circuitry interacting with peripheral mechanics, the proponents, largely by inference, have extended the theory to include the higher-level processes that generate descending commands to the spinal cord (Ostry & Feldman, 2003). In fact, an essential limitation to EPH is the injunction imposed by its proponents against the supraspinal nervous system modeling, computing, or predicting dynamics. This point seems to reflect a philosophical preference of the authors, rather than a rigorous consideration of the EP model. There is no question that calculations of formal dynamics using symbolic math do not occur in the CNS, except through declarative cognitive processes. Nevertheless, the evidence that humans take account of dynamic factors for motor selection and motor control is overwhelming. This includes evidence from adaptation studies showing generalization of dynamics and aftereffects reflecting previously applied loads (Dizio & Lackner, 1995, Conditt et al., 1997, Ghez et al., 1999, Sainburg et al., 1999, Hinder & Milner, 2003, Hwang & Shadmehr, 2005), evidence that humans often select actions that have reduced energetic requirements (Alexander, 1997, Massaad et al., 2007, Nishii & Taniai, 2009), evidence for hemispheric asymmetries in accounting for dynamics in coordination of reaching, an effect that is hard to explain if the central nervous system does not account for dynamics (Sainburg & Kalakanis, 2000, Bagesteiro & Sainburg, 2002, Sainburg 2002, Sainburg & Schaefer, 2004, Schabowsky et al., 2007, Schaefer et al., 2007, Schaefer et al., 2009, Mutha et al., 2012, Przybyla et al., 2012, Schaefer et al., 2012, Coelho et al., 2013, Mani et al., 2013), evidence that we account for the effects of inertial dynamics when making point to point targeted movements (Ghez et al., 1990, Sainburg et al., 1993, Gordon et al., 1994a,b, Ghez & Sainburg 1995, Sainburg et al., 1995), and evidence that we predict object behavior based on physical properties (Dingwell et al., 2002, Dingwell et al., 2004, Cothros et al., 2006, Kluzik et al., 2008, Chib et al., 2009). None of these observations precludes the idea that movement must ultimately be controlled by specification of joint, limb, and body referent configurations. However, the EPH proponents find the idea of internal models of physical phenomenon to be distasteful, seemingly due to philosophical reasons.

There are a variety of unresolved limitations to this hypothesis that have been debated in the literature for many years, including whether muscle resistance to displacement (often referred to as muscle stiffness) measured during movement is large enough to support this form of control (Gomi & Kawato, 1997, Popescu & Rymer, 2000, Hinder & Milner, 2003, Popescu & Rymeri, 2003), and violations in equifinality predictions (Popescu & Rymer, 2000, Sainburg et al., 2003). However, it should be stressed that the assumptions of equifinality are based on nonbiological mass-spring systems, and should not be assumed for all cases of biological control because muscle force-length properties, as well as sensorimotor responses, are largely nonlinear (see Feldman & Latash, 2005). Nichols and colleagues have recently demonstrated that heterogenous inhibitory force feedback from tendon organs can alter the slope of the muscle length tension relationship, calling into question its invariance and relegating a single threshold/length variable (lambda) inadequate to support control (Nichols & Ross, 2009). With regard to the complexity and variety of spinal circuits (Tresch et al., 1999, Loeb, 2001), the EPH has no explicit description of how all these might be integrated to yield a unique and stable equilibrium position for a given motor neuron threshold.

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An important empirical limitation of EPH is the measurement of the invariant characteristic, which needs to be done under a constant central state. However, there has been no formal method to assure this can be done. In humans, the strategy has been to tell people, 'do not intervene' (or some similar instruction), and assume that this stabilizes central commands to muscles (Latash, 1992, Archambault et al., 2005). A common, though anecdotal, demonstration of referent configuration involves the unloading response: a weight, such as a book supported on the hand with the forearm held out straight, is removed from the hand. The typical response is that the elbow immediately flexes and achieves a new, more flexed, position. This position is described as the specified referent configuration for the elbow when holding the book. However, an alternative explanation is that the static equilibrium between elbow flexor force, and gravitational load is disrupted, producing elbow flexor acceleration. Flexor motion elicits an extensor stretch reflex, which brings the limb to a stop and allows the subject to achieve a new equilibrium between elbow force and gravitational load. This sequence does not require a predetermined referent configuration. The argument against this interpretation is that subjects were told not to intervene, which may or may not be effective in preventing voluntary actions. However, the effects described do not require declarative cognitive mediation. In fact, a demonstration that argues against the EPH description of the unloading experiment is a condition in which a very large load is held by near maximal elbow torque, such as a heavy dumbbell. The required referent configuration for such a large torque would be outside of the anatomical range of the limb. Nevertheless, unloading the arm does not accelerate the limb into its full range, even if people are told not to intervene. Rather a new position is achieved in an intermediate range. Therefore, even though subjects are told, "do not intervene", their limb is not displaced to the extreme of the anatomical range. Instead, subjects achieve a comfortable posture, which certainly does not reflect the referent configuration for supporting the dumbbell before unloading.

In summary, the EPH has proved to be an elegant and generative hypothesis in motor control research. It is currently the only hypothesis that resolves the posture-movement paradox, integrating the control of posture and movement into a single control scheme. However, the claim that this hypothesis has reached the status of a scientific theory seems premature. Many aspects of motor control remain unexplained by EPH, and some phenomena appear to contradict this hypothesis., Therefore, the predictive and explanatory power of EPH remains too limited to consider it an accepted scientific theory, at this point in time.

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